The Journal of Parasitology

Volume 22 OCTOBER, 1936 Number 5

A COMPARATIVE STUDY OF THE FIRST-INSTAR LARVAE OF THE GENUS *SARCOPHAGA* (CALLIPHORIDAE, DIPTERA), WITH NOTES ON THE BIOLOGY

By Edward F. Knipling[1]

Division of Insects Affecting Man and Animals, Bureau of Entomology and Plant Quarantine, United States Department of Agriculture

Dipterologists have, by extensive study, made many important contributions which facilitate the specific determination of adults in the genus *Sarcophaga*. Unfortunately, they have given little attention to the characteristics by which the different species may be distinguished in the immature stages. The economic importance of the Sarcophaginae is largely due to the damages resulting from, or benefits derived from, the feeding habits of the larvae. Therefore, from an economic standpoint, it is equally as important, or even more so, to recognize the species in the larval stage as it is in the adult. Frequently species of *Sarcophaga* are implicated in myiasis in man and animals. Since the present lack of knowledge on the subject necessitates the rearing of larvae to the adult stage in order that males for determination may be secured, many cases remain undetermined. This paper records a comparative study of 24 species in the first larval instar. Four of these are not specifically determined but are included primarily to show further morphological variations in the genus. All of the species studied show definite specific characteristics, and no doubt further study will show that a large majority of the species may be specifically determined. In some species differences are even more pronounced in the first larval instar than in the adult stage.

[1] The writer is indebted to those who have given aid during the course of these investigations. Thanks are due to the following members of the Bureau of Entomology and Plant Quarantine, United States Department of Agriculture: To E. W. Laake, Entomologist, for the loan of specimens of larvae and for worthy suggestions; to F. C. Bishopp, Principal Entomologist, and R. W. Wells, Associate Entomologist, for helpful suggestions and criticisms; and especially to D. G. Hall, Assistant Entomologist, for determining or verifying determinations of numerous adult specimens of Sarcophaginae, and for valuable suggestions relating to this study.

Root (9),[2] in a comparative study of several representatives of the genus *Sarcophaga,* pointed out that larvae in the third instar show specific differences. In addition to the present studies of the first-instar larvae, a superficial examination of over 25 species in the third instar bear out Root's contentions that species may be readily recognized in the larval stages.

The first-instar larvae of *Sarcophaga haemorrhoidalis* Fallen has been described by Keilen (6) and Moutia (7), and illustrated by Tao (11), Patton (8) has described the first instar of *S. fuscicauda* Boettcher. The cephalopharyngeal mechanism and posterior spiracles of *S. securifera* Vill. in the three instars have been figured by Smith (10).

Although some consideration has been given the third instar, a very small percentage of the species have been described in this stage. Furthermore, it is doubtful if all of the available descriptions are sufficiently comprehensive to enable closely related forms to be distinguished. Banks (2) described the last-instar larvae of several representatives of the genus. Several species have been briefly described by Patton (8). Root (9) made a comparative study of a number of species and pointed out that specific diagnostic characters may be established even in such closely related species as *Sarcophaga lherminieri* R. D. (*communis* Park.) and *S. sueta* v. d. Wulp (*communis* var. *ochracea* Ald.). The most comprehensive work, however, on the immature stages of the genus *Sarcophaga* and related genera is that of Greene (3), which consists of descriptions and figures of the third instar of *S. cistudinis* Ald., *S. placida* Ald., *S. bullata* Park., *S. securifera* Vill., *Wohlfahrtia vigil* Walk., and of the pupal stages of 41 species.

In addition to making specific identifications possible, a comparative study of the larvae will undoubtedly aid in the determination of the true relationship of species. It is probable that the large genus *Sarcophaga* will eventually be divided into smaller genera, or at least divided into more definite groups. It is not the desire of the writer to propose these groups, for to do this efficiently would require the study of a larger number of species in both larval and adult stages. It may be stated here, however, that the study of the first larval stages shows that certain species tend to fall into definite morphological groups.

The first-instar larvae of different species within the genus *Sarcophaga* show much greater morphological variations than do those of the separate genera *Lucilia, Calliphora,* and *Cynomyia.* For example, the first-instar larvae of *Lucilia, Calliphora,* and *Cynomyia* have more in common than do specimens of *S. galeata* Ald., *S. pusiola* v. d. Wulp,

[2] Numbers in parenthesis refer to the publications given in the list of references.

S. haemorrhoidalis Fall., *S. sueta* v. d. Wulp, *S. utilis* Ald., *S. plinthopyga* Wied., *S. impar* Ald., *S. cimbicis* Towns., and the species of the "prohibita"[3] groups, as well as others included in this study. Likewise, the genera *Phormia, Protophormia,* and *Cochliomyia,* on the basis of larval similarities, form a more homogeneous group than do some of the species incorporated in the genus *Sarcophaga.*

HABITS AND LIFE HISTORY

Within the genus, there is evident a great variation in the feeding habits of the larvae; some normally breed in animal excrement, others are principally necrobionts, while still others are parasitic on insects and other animals. Aldrich (1) and Hall (4) record the breeding of a large number of species. The species collected by the writer were reared on decaying meats or animal excrements. The species *S. kellyi* Ald. *S. rapax* Walk., *S. latisterna* Park., *S. cimbicis* Towns., and others which readily complete development in decaying meats have also been recorded as parasites of insects. Thus it may be seen that variations in habits may be found within a species as well as in the genus as a whole. Some forms, however, such as those in the "prohibita" group, apparently are obligate parasites on insects or other animals, since they have been previously reported as parasitic and recent efforts to rear larvae of this group on several types of media were unsuccessful. The media used in rearing the various species are given under the descriptions of these species.

All of the species collected are viviparous. The embryo develops in the gravid female and is generally deposited while still within the egg membrane. Almost immediately after deposition the larvae break out and disappear within the available food material. Frequently undeveloped larvae, and occasionally even ova that apparently do not contain developing embryos (owing to lack of fertilization or other causes), are deposited along with normally developed larvae. This has been noted by Hall (5) and by Smith (10). Larvae that are not fully developed will remain encased within the egg membrane, under favorable conditions, until they are fully developed. The immature embryos will easily desiccate, however, and unless in a humid atmosphere will die before they are ready to begin feeding.

In a number of species ova were squeezed from the fly before the embryos were visible and were placed in a vial plugged with moist cotton. In every instance most of the ova so treated developed into fully

[3] A group of closely allied sarcophagid flies, possessing a distinct larvipositor, frequently reared from insects. The group contains such species os *S. prohibita, S. hamata, S. excisa, S. alcedo,* and others. The so-called "prohibita" group also includes the species placed in the genus *Blaesoxipha* by Palearctic dipterists.

matured embryos. More often, after it was determined that the ova did not contain mature embryos, they were allowed to remain within the body of the dead fly. The fly was then placed in a vial plugged with moist cotton, and when treated in this manner the ova generally developed into fully matured embryos within 24 to 48 hours. These larvae fed and completed their development when placed on a favorable medium. The species in which this was successfully accomplished were: *S. ventricosa* v. d. Wulp, *S. lherminieri* R. D., *S. haemorrhoidalis* Fall., *S. pusiola* v. d. Wulp, *S. stimulans* Walk., *S. misera* var. *sarracenioides* Ald., *S. bullata* Park., *Sarcophaga* sp., and *Sarcophaga "B."* Deposition of eggs, as in true oviparous Diptera, was not noted in nature, although the deposition of larvae was frequently noted when gravid flies were being collected, and, except for the occasional infertile ova and those containing immature embryos, the deposited larvae immediately became active and disappeared within the available food material.

The number of larvae deposited varied greatly with the different species. Records were based on the number of larvae squeezed from gravid females captured in nature. It is probable that some of the flies had deposited some of the larvae before being captured; however, the average number of larvae thus secured from a number of females may be a fair index to the number normally produced by the various species in nature.

Sarcophaga sp. produced the smallest number of larvae, the average of five females being 6.4. The average number in other species in which records were obtained from five or more females was: *S. utilis* Ald., 6 females, 18; *S. impar* Ald., 6 females 21; *S. lherminieri* R. D., 5 females, 29.6; *S. misera* var. *sarracenioides* Ald., 9 females, 36; *S. haemorrhoidalis* Fall., 5 females, 43.2; and *S. bullata* Park, 8 females, 103. In one undetermined species belonging to the "prohibita" group, 213 larvae were collected from one female and in another species 325 larvae were taken from a single gravid female. It may be seen from these records that the number of larvae produced may vary from approximately 6 to over 300. The majority of the species, however, produced between 20 and 40 larvae. The variations in each of the above species and others not mentioned here are given under description of species.

Larvae deposited by the gravid female are generally forced through the larvipositor with the anterior end foremost. In some cases, however, they may be deposited with either the anterior or posterior end in advance. The usual manner of locomotion following deposition is with the anterior end forward, but interesting observations on one species, *Sarcophaga* "C," show that the direction of movement may be reversed. Morphologically, this species is better adapted for this mode of travel since the anteriorly directed spines are well developed, while the spines

directed posteriorly are minute. Another species, *Sarcophaga "B,"* probably has this same habit, although no movement was noted, since the spines directed anteriorly are by far more highly developed (figure 46) and would undoubtedly interfere with movement of the larva with the anterior end forward.

The life cycle from larva to adult may be less than 11 days. In one instance larvae of *S. stimulans* Walk. were collected and placed on cow manure at 2 p. m., July 11. By 11 a. m. the following day, or in 21 hours, the larvae were beginning to transform to the third instar. Pupation began by 10 a. m. July 16, or in less than 4 days. Adults emerged at 8 a. m., July 22, a period of 10 days and 18 hours from larva to adult. Larvae of *S. imper* Ald. collected at the same time and placed on decomposing meat emerged as adults on the 14th day. Other life-history records are contained in the descriptions of species.

Some of the species of *Sarcophaga,* and possibly all of them, overwinter as pupae in Iowa. During the latter part of September to October developing larvae pupate but then go into a state of hibernation and even under ordinary room temperatures will not emerge as adults until late in the winter or early in the spring. The following species have been observed in this state: *S. ventricosa* v. d. Wulp., *S. lherminieri* R. D., *S. pectinata* Ald., *S. bullata* Park., *S. importuna* Walk., and *S. haemorrhoidalis* Fallen. Some of the Calliphorinae, such as *Lucilia* and *Cynomyia,* on the other hand, overwinter as larvae.

Technique

Adult females of the genus *Sarcophaga* are not readily distinguished from closely allied species. To establish the correct identity of the larvae collected, it is therefore necessary to allow some of the larvae to complete development in order to obtain males for determinations.

Gravid females were captured in flytraps, or while feeding on decaying meats or other refuse, and, in some cases, while resting on plants or other objects. By lightly squeezing the abdomen of the gravid fly, the larvae are usually forced out. (There are exceptions, however, as in the species *S. haemorrhoidalis,* in which the larvae cannot be forced out by applying pressure to the abdomen of the fly.) Larvae collected in this manner were kept in water, until ready for placement on breeding media, and frequently left for several hours, in some cases as many as 24, without apparent harm. On the other hand, newly emerged larvae soon desiccated in the absence of free moisture.

Before the more abundant species were recognized, larvae were reared from all the gravid females collected. Since some of the more common species are frequently collected, this method necessarily resulted in many duplicate rearings. To enable the detection of any possible

variations in characteristics, however, a number of series of larvae of the same species was desirable.

After gravid females were collected indiscriminately, some of the first-instar larvae of the desired species were preserved and the remainder of the desired species were placed on the chosen media for further development. For rearing purposes the larvae were placed on the food in pint or quart jars partly filled with moist sand. In order to keep the strain of these larvae pure, the jar was provided with either gauze or a 36-mesh copper-screen top and kept in the laboratory or placed outdoors in a 14-mesh screen cage. Specimens of second and third instar larvae were taken as they developed and preserved for future study. Some larvae in each case were allowed to complete development in order that adult males might be secured, on which the identity of the larvae depended.

All of the larvae collected were of the first generation and no attempts were made to rear and collect larvae of the second generation.

Collected larvae were killed in hot water and preserved in 70 to 80 per cent alcohol until such time as it was convenient to study them.

A detailed study of the larval characters under high magnification necessitates cleared and mounted specimens. The larvae were heated in 5 to 10 per cent potassium hydroxide solution until the softer inner tissues were disintegrated to the extent that they would either come out by the agitation of the boiling solution or could be readily forced out by external pressure. Then the cleared larval cuticle together with the cephalopharyngeal mechanism was thoroughly washed in tap and distilled water, after which it was dehydrated in 70, 80, and 95 per cent and absolute alcohol, cleared in xylol, and mounted in balsam on a glass slide. Each larva thus treated was then placed laterally on a glass slide in balsam. All the folds were smoothed out as much as possible and the cover glass was pressed lightly on the larva in order not to disturb the normal form of the cephalopharyngeal sclerites. Well cleared specimens free of folds are necessary in order that the distribution of spines, which is one of the most useful characters, may be accurately determined.

Figures of the cephalopharyngeal mechanism and posterior spiracles were made with the aid of a camera lucida.

LARVAL CHARACTERS

The larvae present a number of useful characters which aid in distinguishing the species. One has only to compare the structure of the cephalopharyngeal mechanism of the different known species to appreciate the morphological variations of this structure in the group. Other characters, though in general not so useful as the cephalopharyngeal sclerites, also show striking specific differences. The more important

characters used in the descriptions, in addition to the cephalopharyngeal skeleton, are: Size and general appearance of the larvae; shape, size, and distribution of spines; and size and shape of posterior spiracles. Other less important diagnostic characters are the size of the posterior cavity and size and number of the papillae on the border, general appearance of anal area, and structure of the first apparent or cephalic segment.

Size and general appearance of larva. The size of the larva as given in the description is the size fully extended, as when taken from the fly, before postdeposition growth has taken place. For this reason this character will be of limited value, for after feeding the size of the larva rapidly increases. The application of this character, therefore, will be limited to larvae collected from the gravid female or very soon after deposition. In rare instances, this character may aid in identifying gravid female flies by means of the larvae. The size of newly deposited larvae varies greatly between species; for example, newly deposited larvae of *S. pusiola* v. d. Wulp. measure approximately 2 mm., while those of *S. utilis* Ald. measure approximately 4.5 mm., and those of *Sarcophaga* sp., the largest newly deposited first-instar larvae collected, measure approximately 7 mm.

Although the general form of the larva is of little specific value, there are some characteristics more or less common to certain groups of closely allied species which may be an aid in identification. The various species are figured in plates 3 and 4.

Shape, size, and distribution of spines. The size of the spines may vary from those of approximately equal length and breadth to those many times as long and as broad. The number of points per spine varies with the species. The form and comparative size of spines may be noted by examining figures 61–77.

The distribution of spines is one of the most reliable characters, but in order to see accurately this distribution, well mounted larvae are necessary, and these in some cases are difficult to obtain. All of the larvae of the group possess small recurved spines, usually near the anterior or posterior margin of the segments. The spines are generally in more or less irregular, closely approximated rows, forming a band or bands on each segment. The following spinose characteristics are useful in separating the species: The number of segments which possess a complete band of spines encircling the body at either the anterior or posterior border or at both, the number of rows in the band, and the relative position of spines in the rows. The distribution of spines on the various species may be noted by examining the partly diagrammatic arrangement in figures 28 to 46. Figures 47 to 60 are more enlarged and show the arrangement of spines in the dorso-lateral region in a number of species; figures 78 to 90 show the arrangement of spines on the ventral surface.

Posterior spiracles. On the last apparent segment, situated in a depressed area or posterior cavity, are located the pair of posterior spiracles. Each spiracle has two spiracular slits very nearly contiguous at the lower ends, which may or may not be surrounded by a ring or peritreme (figures 24 and 25). The general opinion is that the first-instar larvae of the Calliphoridae do not possess a ring or peritreme surrounding the slits. This is not true for all of the species of *Sarcophaga,* since the peritreme is especially prominent in *S. galeata* Ald. and *S. ventricosa* v. d. Wulp, as the figures indicate. In some of the related species an indistinct peritreme is usually visible, and in others there is no indication of a peritreme except for a small pigmented area below the slits which corresponds to the lower portion of the peritreme. The spiracllar slits of the necrophagous and parasitic species are totally without a peritreme. The appearance and size of the spiracular slits are of some value in identification.

Cephalopharyngeal mechanism. The sclerites that make up the cephalopharyngeal skeleton (figures 1–23) situated in the anterior segments of the larva furnish the most dependable character for specific determination. Size and structure are the most important points to be noted. The degree of pigmentation, although rather variable, depending on the age of the larva, is also of some value.

Posterior cavity. The last apparent segment possesses a depressed area in which, as previously mentioned, are situated the posterior spiracles. The size of this cavity is sometimes of value, but the arrangement of spines on the border and the small tubercles situated on the border above and below the depression are more useful characters. Six pairs of tubercles are generally present in the third-instar larvae of Calliphoridae; three pairs are situated above and three below the cavity. In the first-instar of *Sarcophaga,* however, all six pairs are seldom evident, more often being reduced to two pairs above and two below the cavity. In *S. galeata* Ald., *S. ventricosa* v. d. Wulp, and others, which possess numerous long hair-like spines on the border of the last segment, each tubercle appears as a small circular spineless area (*T,* figure 28).

Anal area. On the last apparent segment, ventrally, near the posterior border, is situated the anal opening. Surrounding the opening is a swollen area, generally more or less irregular, the size and shape of which show considerable variation. Usually, a single pair of fleshy lobes or tubercles, one on each side of the area, extends laterally, but in some species two additional posteriorly directed tubercles are situated one on each side of the anal opening and the lateral tubercle. These posteriorly directed tubercles, if present, are generally small and indistinct in first-instar larvae; in the second and third instars, however, they are very prominent. The tubercles are easily forced out of shape, so this char-

acter is of no value in mounted specimens, although it is a good diagnostic character in well relaxed unmounted material.

DISCUSSION

For the most part, larvae treated in this manuscript were collected and reared from gravid females taken in the vicinity of Galesburg, Illinois; Ames, Iowa; and Dallas, Menard, and Port Lavaca, Texas; the majority being from Galesburg, Illinois, and Ames, Iowa.

When one considers all of the species of *Sarcophaga* described from the United States, the number represented in this study appears comparatively small. In general, the species included here are the more abundant and widespread forms and therefore those more commonly collected. In the Middle West, in particular, the majority of the specimens of larvae collected at random in nature would probably be found to belong to the species here treated. On this assumption, for identifying specimens, this work should be of greater practical value than the actual number of species would seem to indicate. The following species of *Sarcophaga* were taken in flytraps baited with liver and operated throughout the active fly season, in the vicinity of Ames, Iowa, during 1933; *S. ventricosa* v. d. Wulp, *S. bullata* Park., *S. lherminieri* R. D., *S. utilis* Ald., *S. misera* var. *sarracenioides* Ald., *S. stimulans* Walk., *S. haemorrhoidalis* Fall., *S. planifrons* Ald., *S. pusiola* v. d. Wulp., *S. latisetosa* Park., *S. impar* Ald., *S. barbata* Thom., and three undetermined species. In addition to the above, the following species have been collected other than by means of flytraps: *S. sinuata* Meig., *S. importuna* Walk. (*pachyprocta* Park.), *S. reversa* Ald., *S. cimbicis* Towns., *S. rapax* Walk., and *S. kellyi* Ald. Of all these species only *S. latisetosa, S. reversa, S. sinuata, S. importuna,* and the three undetermined species are unrepresented in this study. The larvae of *S. sinuata* and *S. importuna* have been reared, but too late to be incorporated in this manuscript. No doubt there are many other species in Iowa. Hall (4) records 38 species of Sarcophaginae from Kansas and lists 21 additional species collected in bordering States, which likely occur in Kansas; but, generally speaking, those species included in this study are the most common in Iowa.

As previously mentioned, the larvae fall into groups rather easily on the basis of morphological similarities. The three species *S. galeata* Ald., *S. ventricosa* v. d. Wulp, and *S. australis* Ald. are very closely allied and, except for minor details, are similar in structure of cephalopharyngeal mechanism, general form and structure of body, structure and distribution of spines, and general appearance of posterior spiracles. *S. pusiola* v. d. Wulp is distinct from other species, differing principally in structure and distribution of spines. *S. stimulans* Walk. and *S. laakei* Hall, although not so similar as the two groups mentioned, show close

relationship. This is likewise true for *S. lherminieri* R. D. and *S. sueta* v. d. Wulp.

All of the above have much in common, having the same general form of body, reduced spines at anterior border of segment 3, and in general a similar type of cephalopharyngeal sclerites, and all have similar breeding habits. They are all manure-breeding forms, although some of the species have been reared on decomposing meats in the laboratory.

The first-instar larva of *S. haemorrhoidalis,* although quite different in many respects, appears to be more closely allied to the coprophagous species than to the necrobionts. The adults, on the other hand, apparently show no relationship to the excrement feeders. In correspondence, D. G. Hall states: "There is little in the morphology of either the male or female of *haemorrhoidalis* to suggest close relationship to the 'pallinervis group'." (A group which includes most of the species mentioned above.) The species *S. haemorrhoidalis* is commonly found breeding in decaying meats and seemingly this is the preferred breeding place. It is not uncommon in nature, however, to see the females depositing larvae on animal excrement of various kinds. This has been observed by the writer on numerous occasions.

In structure and distribution of the spiny armature and in general form of the body *S. haemorrhoidalis* shows closer relationship to the typical excrement-feeding forms than to the meat feeders. The cephalopharyngeal mechanism shows little resemblance to that of either group, but has one characteristic common to the excrement-feeding species. This character is in the development of the ventral cornu, which is produced ventrally and posteriorly by a narrowed pigmented strip slightly enlarged at the end.

Since larvae of *S. haemorrhoidalis* show some morphological characteristics common to excrement-feeding forms and since its feeding habits are considered to be principally those of necrobionts it is probable that the species is in a state of transition from an excrement feeder to a decomposing-meat feeder. This species has been recorded from a number of cases of intestinal myiasis in man and is thought to be largely responsible for such cases caused by the larvae of Sarcophaginae.

Following the species mentioned, *S. utilis* Ald., *Sarcophaga* sp., and *S. misera* var. *sarracenioides* Ald. appear to be closely allied on the basis of similarity in structure of cephalopharyngeal sclerites (figures 9, 10, and 11). In structure and distribution of spines, however, *S. misera* var. *sarracenioides* shows no relationship to the other two species, but instead is almost identical with *S. impar* Ald., which, on the other hand, differs greatly in structure of cephalopharyngeal mechanism. *S. imper* shows evidence of close relationship to *S. kellyi* Ald., but differs appreciably in many respects.

The four species *S. plinthopyga* Wied., *S. barbata* Thom., *S. securifera* Vill., and *S. bullata* Park. are closely allied, having a similar type of cephalopharyngeal sclerites and, in general, showing similarities in structure of spines. *S. barbata* and *S. securifera,* especially, are closely allied in these respects. These four species of *Sarcophaga* may often be found in cases of dermal myiasis in man and animals.

S. rapax Walk. is more or less distinct from other species included in this study.

The two species *S. latisterna* Park. and *S. cimbicis* Towns. are two closely allied forms and in structure of spines and cephalopharyngeal mechanism are unique. Another species, *S. importuna* Walker (*pachyprocta* Park.), not included in this study, is similar to these two, having the same type of spines and cephalopharyngeal sclerites.

The three species *Sarcophaga "A", Sarcophaga "B",* and *Sarcophaga "C"* are members of the so-called "prohibita" group. A number of undetermined species of this group were collected and the three mentioned above were chosen for comparative study. They differ considerably in structure of cephalopharyngeal sclerites and more so in structure of spiny armature. The one outstanding character common to all of the species of this group is in the structure of the posterior spiracles, which are of the type shown for *Sarcophaga "B"* (figure 27).

As more species of larvae are studied, the author believes that the relationship between species and definite groups may be established, which will be an aid to taxonomists in determining limitations to various groups on the basis of adult characters.

GENERAL DESCRIPTION

The larvae are of normal muscoid shape, tapering anteriorly from about the middle, cylindrical to slightly tapering posteriorly, the cephalic segment ending in two prominent maxillary lobes each with two small papillae (photo-receptive organs) situated one above the other. Below, on the cephalic segment, is situated the mouth orifice and on each side is located the stomal disc, which possesses striations that lead to and converge into the mouth. In most coprophagous species there is a band made up of short parallel tubular structures which starts on each side of the mouth near the dorsal surface and leads to the oral opening, the prominence of this structure varying with the degree of pigmentation. At the posterior end of the larva is located a depressed area, the posterior cavity, the size and depth of which vary with different larvae, and in some of the parasitic forms it is almost totally lacking. Small fleshy projections or tubercles are situated on the borders above and below the cavity; the number of well-defined tubercles is variable but generally there are two pairs above and two pairs below the posterior cavity. Below on the last

apparent segment is an enlarged portion known as the anal area, of variable size in different species. On each side the anal area generally terminates in a rather sharp lateral tubercle. An additional pair may be present above the lateral tubercles.

Anterior spiracles (metapneustic) are lacking. Two posterior spiracles are situated in the posterior cavity; each with two elongate, generally slightly oval slits, almost contiguous at the lower end. In the species of the "prohibita" group the slits terminate in sharp points. Spiracular slits may be surrounded by a ring or peritreme, but more often this is lacking.

For convenience only 12 segments will be considered; these are numbered in order beginning with the first apparent or cephalic and ending with the twelfth or last apparent segment (figure 28). The second, third, and fourth apparent segments are generally considered the first, second, and third thoracic segments, respectively, while the fifth to the twelfth are the first eight body segments. The anal area is composed of the ninth and the tenth body segments, but here they are considered a part of the twelfth or last apparent segment.

The larvae are generally armed with spines, which are spaced in irregular, closely approximated rows in the form of bands, situated near the border at either the anterior or the posterior end of the segments. The spines at the anterior border are recurved posteriorly, while those at the posterior border are recurved anteriorly.

At the anterior border of segment 2 the band of spines is generally widest ventrally. On segments 3–5 the band is approximately the same width throughout, but beginning on segment 6 it is widest ventrally and is made up of several rows of posteriorly directed spines generally separated by a transverse spineless area. Several rows of anteriorly directed spines on the posterior border of the preceding segment appear as a part of the broadened band of spines on the anterior border. Figures 78–91 show the arrangement of spines ventrally to ventro-laterally in a number of species. Laterally on segments 5–12 a small fusiform pad (*LF*, figure 28) is located which is generally provided with spines. All segments are provided with spines on the ventral surface. The number of segments with spines at the anterior and posterior borders varies dorsally and laterally with the species.

Spines in the band at the anterior border of each segment are generally largest in anterior rows and decrease in size in posterior rows. Figures 47–60 show the arrangement of spines in the band near the anterior dorsal surface of segments 5 or 6. On the posterior border the spines decrease in size anteriorly. More often than not they have a single point; spines with two or three points, however, are present in several species and in *S. cimbicis* and *S. latisterna* there may be eight or more points

per spine on the ventral fusiform areas. The comparative size and structure of spines in different species may be noted by comparing figures 61–77.

The structure of the cephalopharyngeal mechanism situated in the anterior segments may best be understood by examining figures 1–23.

DESCRIPTION OF SPECIES

In the description only the more important characters which are not figured are described. To avoid lengthy descriptions and to conserve space, reference is made to the figures whenever practical.

The length of the larva refers to the length, fully relaxed, as it is when taken from the gravid fly. Measurements of spines were made from near the dorsal surface and apply only to the larger spines in the region from which measurements were made. The two spiracular slits are generally unequal in length, although the difference is slight in most of the species. Except where measurements of both are given, the length refers to the longest slit. The length of the cephalopharyngeal skeleton is from the tip of the oral hooks to the posterior extremity of the dorsal cornu, and the width is from the dorsal to the ventral edge of the pharyngeal sclerites, midway between the piece that connects the dorsal and ventral cornua.

Figures showing the arrangement of spines were made from near the dorsal region at the anterior border of segment 5 (segment 6 for *S. sueta* and *S. lherminieri*), and ventrally on segment 8; therefore, reference to the arrangement of spines will apply only to these two regions, although the ventral spines are similarly arranged on segments 6–12.

The first-instar larvae of the genus *Sarcophaga* may be readily distinguished from the second and third instars by the following characters: (1) The anterior spiracles are absent in the first instar; (2) the dorsal cornua are one solid piece, whereas in the second and third instars they are deeply incised posteriorly to form a dorsal and a ventral accessory piece; (3) the posterior spiracles in the third instar are provided with three slits; both the first and second instars have two slits to the spiracle, with the slits more widely separated in the second instar; (4) the spiracular slits in the second and third instars are always provided with a pigmented ring which is incomplete ventrad of the slits, whereas in the first instar the ring is more often absent entirely (if present, it completely encircles the slits or at least is not incomplete ventrally).

Other differences are readily apparent to one familiar with the various instars; those mentioned, however, will suffice in making the distinction.

First-instar larvae of the genus *Sarcophaga* may be distinguished from those of other species of Calliphorids by the deep posterior cavity and by the uniformly developed oral hooks.

Sarcophaga galeata Aldrich

Length of newly deposited larvae 3.78 mm. Anterior half-tapering cephalically, posterior half cylindrical except for last apparent segment, which is enlarged owing to the prominent anal area. Four fleshy projections or tubercles on anal area, one on each side directed laterally and dorsally and a smaller one on each side of anal opening directed posteriorly. Posterior cavity large, with transverse diameter almost equal to width of segment. Two pairs of small, well defined, circular, spineless areas on upper border representing tubercular structures; a single pair situated on lower border. Cephalic segment comparatively small, ending in two prominent maxillary lobes, each bearing a pair of small papillae or photo-receptive organs (*PO*, figure 28). On the under side of the cephalic segment on each side of the oral aperture is a prominent, curved, brownish band-like structure (*OB*, figure 28) made up of short, parallel, closely approximated, tubular structures, which are shortest near the dorso-lateral surface, making the band narrow at this point. The band gradually becomes broader toward the ventral surface, where it forms an inverted U-shaped structure, ending at the border of the oral opening near the lower portion of the mouth. This prominent oral band will immediately distinguish this species, and the two following, from all others included in this study.

Body heavily armed with broad bands of spines; anterior border of segments 2–11 provided with posteriorly directed dorsal and ventral spines; beginning on segment 5, opposite the lateral fusiform pads, the band of spines becomes narrower on each succeeding segment posteriorly, the band being interrupted by a spineless area on segments 10 and 11; on segment 12, at the anterior border, spines present only on ventral and ventro-lateral surface, and a few scattered spines dorso-laterally. Posterior border of segments 5–7 provided with anteriorly directed spines dorsally and ventrally, which are not present for a short space above the lateral fusiform area; on segments 8 and the following the spines completely encircle the segments; on the border of the last apparent segment the band is very broad and made up of long hair-like spines 40–50 microns in length. Arrangement of spines in band on segment 5 as in figure 47, similar on all segments; arrangement ventrally on segment 8 as in figure 78. The band of spines at the anterior border of segment 2 somewhat narrowed and with lighter colored spines than on the succeeding segments. General form of spines similar on all segments; long, narrow at base, and gradually tapering to a point (figure 61). Length of longest spines, near dorsum, on anterior border of segment 6, 30 microns; on posterior border of segment 11, 36 microns.

Posterior spiracles each with two spiracular slits completely sur-

rounded by prominent ring or peritreme (figure 24). Length of plate 114 microns, width 82 microns.

Cephalopharyngeal mechanism as shown in figure 1. Length from tip of oral hooks to posterior extremity of dorsal cornu 744 microns; width from dorsal edge to ventral edge, midway between the narrowed portion of pharyngeal sclerite, 152 microns. Tip of oral hook slightly serrate, as shown in more enlarged figure of oral hooks.

Specimens collected and reared at Galesburg, Illinois. Twenty larvae were squeezed from one female. Although normally excrement feeders, the larvae were reared on decaying hamburger meat. The complete developmental period from larva to adult was 14 days, July 14–28.

Sarcophaga ventricosa v. d. Wulp (*assida* Walker)

Closely allied to *S. galeata.* Length of larva 3.2 mm. General form of body, structure of cephalic segment, and last apparent segment as in *galeata.*

Anterior border of segments 2–11 always with spines on dorsal and ventral surfaces; the spines encircle segments 2–10, while on segment 11 the circle is interrupted by a lateral spineless area; segment 12 generally with a few dorsal spines. Posterior border of segments 5–12 with spines; segment 5 with two to three dorsal and ventral rows of spines but lateral spines wanting; on segment 6 the lateral spineless area is more narrow, and beginning on segment 7 the spines form a completely encircling band. Appearance and arrangement of spines as in *S. galeata.* Length of spines on anterior border of segment 6, 24 microns; on posterior border of segment 11, 28 microns.

Posterior spiracular plates with prominent peritreme as in *S. galeata.* Length of plates 88 microns, width 70 microns (figure 25).

Cephalopharyngeal apparatus (figure 2) similar to that of *S. galeata*; length 650 microns; width 130 microns.

Larvae collected at Galesburg, Illinois; Ames, Iowa; and Port Lavaca, Texas. Reared on cow manure and in one case on decomposing hamburger meat. Three females produced 18, 21, and 24 larvae. Developmental period, larva to adult, on hamburger meat, 14 days, July 24–August 8.

Sarcophaga australis Aldrich

Very similar to *S. galeata* and *S. ventricosa.* Length of larva 3.8 mm.

The spines are of the same general type as in the two preceding species, but with narrower bands containing fewer rows of spines (figure 48). Posterior border of segment 5 with a few scattered dorsal spines; lateral spines absent. On each succeeding segment the number of spines

increases and the lateral spineless area decreases until there is a complete band of spines beginning on segment 9. Spines narrow at base and tapering to fine hair-like point; length on segment 6, 24 microns; on posterior border of segment 11, approximately 26 microns.

Posterior spiracles with peritreme surrounding the slits as in *S. galeata,* but decidedly narrower and less pronounced; length of plates 96 microns, width 68 microns. (Not figured.)

Cephalopharyngeal apparatus similar to that of *S. ventricosa*; length 650 microns, width 140 microns. (Not figured.)

Specimens collected at Port Lavaca, Texas. Reared on cow manure.

Sarcophaga pusiola v. d. Wulp (*peniculata* Parker)

Small species. Length 2 mm. Anal area prominent; a pair of small, inconspicuous, posteriorly directed tubercles on each side of the middle in addition to the more prominent lateral pair. Posterior cavity large; two pairs of small spineless areas representing tubercles on both upper and lower border.

Larva heavily armed with spines. Anterior border of segments 2–11 completely encircled with spines; greatly reduced in number dorsally on segment 2 and sparse and lightly pigmented on segment 3. On segments 4, 5, and 6 the spines become darker and form a broader band on each succeeding segment. The bands on segments 7–10 approximately the same width, slightly reduced dorsally on segment 11. Posterior border of segments 3–12 provided with spines; reduced to a few scattered spines in dorsal area on segment 3 and increasing on each of the following segments, joining with ventral spines to form a complete band on segments 5–12. Spines broad at base and tapering to fine hair-like point. Posterior border of last segment with a broad band of long hair-like spines. Length of spines on anterior border of segment 4, 12 microns; of segment 5, 14 microns; of segment 6, 20 microns. At posterior border of segment 11 the spines are longer and more narrowed at base, measuring 26 microns. Arrangement of spines near dorsum on segment 5 and in ventral area on segment 8 as in figures 49 and 79, respectively.

Posterior spiracular slits short and surrounded by a poorly defined peritreme; length of slits 40 microns.

Cephalopharyngeal mechanism as in figure 3, length 409 microns.

Specimens collected at Galesburg, Illinois, and Ames, Iowa. Reared on both decomposing hamburger meat and cow manure. Five females produced 21, 24, 25, 40, and 44 larvae.

Sarcophaga stimulans Walker (*quadrisetosa* Coquillett)

Small species, length 2.4 mm. Form mostly cylindrical, tapering anteriorly from fifth segment. Last segment with prominent rugose anal

area, having a single pair of small tubercles directed posteriorly, as in *pusiola*; lateral tubercles not defined. Posterior cavity large, with two pairs of tubercles on upper and one pair on lower border.

Cephalic segment in region of mouth somewhat similar to that of *S. galeata,* but with broader, less curved, and more lightly pigmented striated area.

Larva heavily armed with spines. Anterior border of segments 2–10 with completely encircling bands, the band on segment 11 incomplete dorsally. Posterior border of segments 7–12 encircled with spines, the width of bands increasing, posteriorly, on each succeeding segment. The dorsal spines are absent on segment 2, or, if present, very lightly pigmented; segment 3, at anterior border without spines except for a narrow ventral band of lightly pigmented spines. Arrangement of spines on segments similar to that in *S. australis;* appearance of spines as in figure 63; similar in form on all segments. Length of spines on segment 6, 10 microns; on posterior border of segment 11, 20 microns. Segment 12 on border of cavity rather heavily armed with long hair-like spines which, on dorsal surface, are arranged in the form of two oval patches that extend anteriorly approximately one-half the length of the segment (figure 31).

Posterior spiracles with faint peritreme surrounding the slits, length 48 microns.

Cephalopharyngeal apparatus as shown in figure 4, small, length 502 microns.

Specimens collected at Ames, Iowa, and Port Lavaca, Texas. Reared on cow manure. Two attempts to rear larvae (apparently this species) on decomposing meats were unsuccessful. Four adult females yielded 20, 24, 28, and 30 larvae. Life cycle discussed under "Habits and Life History," page 7.

Sarcophaga laakei Hall

Length of larvae 2.75 mm. Anal area similar to that of *S. stimulans;* tubercles absent or poorly defined. Posterior cavity large, transverse diameter more than one-half of the width of the segment; upper border with two and lower border with one pair of small tubercles.

Larva well armed with spines. Anterior border of segments 2–10 completely encircled with spines. Spines absent dorsally for a short space on segment 11 and restricted to ventral and lateral surfaces on segment 12, sparse and lightly pigmented on segment 3; degree of pigmentation, length of spines, and width of band increasing on segments 4, 5, and 6, respectively; similar on segments 7–9 and becoming narrower dorsally on segment 10. Posterior border of segments 7–12 provided with spines that form a complete band; on segment 6 the spines are

restricted to the ventral and dorso-lateral surfaces. On segment 12 the spines on the posterior border are distributed as are those on *S. stimulans*, forming a pair of oval patches, which extend anteriorly approximately two-thirds the length of the segment (figure 32). Form of spines as in figure 64; arrangement on segment 5 as shown in figure 50. Length of spines at anterior border of segments 4 and 5, 6 microns; of segment 6, 10–12 microns; on posterior border of segment 11 the spines are longer and more slender, resembling the spines of *S. galeata* (figure 61), becoming shorter anteriorly on each succeeding segment.

Posterior spiracular slits not completely surrounded by peritreme; a rather poorly defined ring extending around the ventral half but disappearing on the dorsal half; slits unequal in length, 56 and 48 microns.

Cephalopharyngeal apparatus as shown in figure 5, length 604 microns.

Specimens collected at Galesburg, Illinois. Reared on decomposing hamburger meat. Three gravid females collected, from which were squeezed 18, 32, and 40 larvae, respectively. Began feeding May 28, pupated June 2, emerged June 13, a developmental period of 16 days.

Sarcophaga lherminieri (Robineau-Desvoidy)
(*communis* Parker) (*pallinervis* Thom.)

Length 3.5 mm. Form similar to that of preceding species. Anal protuberance rather large, rugose, with two small inconspicuous tubercles, one on each side of middle, directed posteriorly. Posterior cavity small; transverse diameter less than half the width of the last segment; lower border of cavity with two pairs of small tubercles; upper border with an inner pair of large leaflike tubercles, a similar median pair, and a smaller outer pair; all closely approximated. In live specimens these tubercles lie flat on the dorsal part of the segment and are generally not prominent, but in fully relaxed preserved specimens and in live specimens in which the posterior end is lightly pressed the tubercular structures are in an upright position and conspicuous. This character alone will distinguish this species from all others included here.

Larvae not heavily armed with spines. Spines at dorsal anterior border of segment 2 lightly pigmented, absent or indistinct on all of segment 3. On segment 4 a narrow band of ventral spines present, poorly defined in dorsal area. Complete spinose band distinct on segments 5–10, but on segment 11 the spines restricted to the ventral and lateral surfaces. On posterior border only segments 10 and 11 encircled with spines, greatly reduced on dorsum of segment 10 and restricted to ventral and lateral surfaces on segment 9; last segment not heavily armed on border of cavity. Arrangement of spines near dorsal part of segment 6 and ventral part of segment 8 as in figures 51 and 81,

respectively. Spines similarly arranged on segment 5 but with a much narrower band. Form of spines on segment 6 as in figure 65; similar at anterior border of all segments. Length of spines: On anterior border of segments 5 and 6, 8 microns; on posterior border of segment 11 the spines are longer and more narrow at end; length 16 microns.

Posterior spiracles without peritreme; below the two slits of each spiracle is a small, irregular, pigmented patch similar to the lower portion of the spiracular peritreme in *S. galeata* and related species; length of slits 76 microns.

Cephalopharyngeal skeleton as in figure 6, length 706 microns.

Specimens collected at Galesburg, Illinois, and Ames, Iowa. Reared on hamburger meat and on cow and horse manure; commonly found breeding in horse manure in nature. From five gravid females 20, 27, 29, 32, and 40 larvae were taken, respectively. Developmental period from larva to adult on hamburger meat 13 days, July 22–August 4.

Sarcophaga sueta v. d. Wulp (*communis* var. *ochracea* Aldrich)

The adult of this species and of *S. lherminieri* are almost identical, but the first-instar larvae are very distinct.

Large species, length 4.26 mm. Form as in figure 33. Anal area prominent, with a small tubercle directed posteriorly near each side; lateral tubercles not defined. Posterior cavity large; more than one-half the width of the last segment; upper border with three small, well defined, conical tubercles; on the lower border the outer and median pairs distinct, the inner pair poorly defined.

Larvae moderately armed with spines; segment 2 and segments 4–11 completely encircled with spines at anterior border of segments; greatly reduced on segment 3, having two or three rows of small, lightly pigmented spines dorsally and laterally but apparently none ventrally. Posterior border of segments 6–12 with dorsal spines; on segment 6 they are reduced to a single dorsal row, increasing in numbers posteriorly on each succeeding segment, and joining with the lateral spines to form a complete ring beginning on segment 9. Form of spines as in figure 66. Arrangement near dorsal surface on segment 6 as in figure 52. Ventral spines on segment 2 with one to two points, occasionally three; a single point on other regions of the body. Spines short; length, on anterior border of segment 5, 5 microns; of segment 6, 6 microns; of segment 8, 10 microns. On posterior border of segment 11 the spines are longer and resemble those of *S. haemorrhoidalis* (figure 67); length on segment 11, 24 microns; segment 10, 16 microns.

Posterior spiracles without peritreme; small, irregular pigmented patch below the slits as in *S. lherminieri;* length of slits 84 microns.

Cephalopharyngeal skeleton as in figure 7, length 781 microns, width 195 microns.

Specimens collected at Port Lavaca, Texas. Reared on cow manure. Fifteen larvae squeezed from one female.

Sarcophaga haemorrhoidalis Fallen

Length of newly deposited larvae 2.90 mm. Anal area moderately large, with a pair of small, laterally directed and a still smaller pair of posteriorly directed tubercles. Diameter of posterior cavity approximately one-half the width of the last segment; two pairs of small circular spineless areas on upper border and one pair on lower border.

Larva heavily armed; anterior border of segments 2–10 and posterior border of segments 6–12 encircled by bands of spines. On segment 3, at the anterior border, the band is greatly reduced; increasing in width on segments 4, 5, and 6, respectively; 7 and 8 of same width as 6 but decreasing on segments 9, 10, and 11, respectively. On segment 11 the dorsal spines absent for a short space. Spines on segments 9, 10, and 11 reduced laterally opposite the lateral fusiform area. Ventral spines arranged as in figure 82. Form of spines near dorsum on segment 6 as in figure 67; long and slender, resembling those of *S. galeata;* form similar on all segments; length, on anterior border of segment 3, 12–16 microns; of segment 4, 20–24 microns; of segment 6, 20–24 microns; on posterior border of segment 11, 28 microns. Ventral spines on segment 2 generally with more than one point; number ranging from one to four with a single point on other segments.

Posterior spiracles without peritreme; length of longest spiracular slit 72 microns, of shortest 68 microns.

Cephalopharyngeal skeleton as shown in figure 8, length 632 microns, width 149 microns.

Specimens collected at Menard, Texas, Galesburg, Illinois, and Ames, Iowa. Reared on decaying meats, and in one case on cow manure. Six gravid females yielded 30, 39, 42, 52, 53, and 64 larvae, respectively. Developmental period larva to adult, 16 days, June 23 to July 9, and on another occasion, 14 days, July 13 to July 27.

Sarcophaga utilis Aldrich

Large; newly deposited larva 4.5 mm. in length. Broadest near the middle, tapering anteriorly and slightly posteriorly. Anal area small, with tubercles each side directed laterally. Posterior cavity large; upper border with two pairs of tubercles, one pair on lower border.

Well armed with spines; anterior border of segments 2–9 completely encircled with spines, dorsal spines absent on segment 10. Posterior border of segments 7–12 provided with spines; on segment 7 the spines

do not completely encircle the segment, being absent for a short space above the lateral fusiform area; band complete on segments 8 to 12, increasing in width on each succeeding segment, except on border of posterior cavity, where the band is narrowed. On segment 2 the spines are equally as dark and the band as broad as, or broader than, on segments 4 and 5, differing in this respect from all other species so far treated. Spines on segment 5 arranged as in figure 53; ventral arrangement on segment 8 as in figure 83. Spines on fourth, fifth, and sixth segments shown in figure 68, *a, b,* and *c,* respectively; length, anterior border segment 3, 12 microns; of segment 4, 20 microns; of segment 5, 22 microns; of segment 6, 26 microns. On posterior border of segments the spines longer; length on segment 11, 34 microns; decreasing in length on each segment anteriorly. All spines with single point. Posterior spiracular slits not surrounded by ring; length of slits 92 microns.

Cephalopharyngeal skeleton very large (figure 9); length 1.044 mm., width 232 microns.

Specimens collected at Galesburg, Illinois, and Ames, Iowa. Reared on decaying meat. Six gravid females produced 6, 12, 15, 16, 29, and 30 larvae.

Sarcophaga sp.

The larva of this species is similar to that of *S. utilis* and, since the adult *S. bishoppi* Aldrich shows close relationship to *S. utilis,* it may be that this larva belongs to the species *S. bishoppi.* The species is included here because it represents the extreme development in size at the time of deposition, and in size of the cephalopharyngeal skeleton. Also, the number of larvae produced by gravid females is less than in any of the other species studied.

Approximate length of larva at time of deposition 7 mm. Heavily armed with large dark spines; anterior border of segments 2–11 completely encircled with spines, but on segment 12 the spines sparse on dorsal and absent on lateral surfaces. The spines become slightly lighter in color and the width of the band on each segment gradually decreases posteriorly. Posterior border of segments 6–11 provided with spines, greatly reduced dorsally on segment 6. Spines long and gradually tapering to a point; length of spines on segment 3, 24 microns; on segment 4, 28 microns; on segment 6, 36 microns; on segment 9, 32 microns; on segment 10, 18 microns; posterior border of segments 11 and 10, 40 microns; of segment 9, 20 microns. Arrangement of spines near dorsum on segments 3–5 similar to that in *S. bullata* (see figure 55); approximately 18 irregular rows of spines each on segments 3, 4, and 5. Ventral spines well developed and longer than near dorsal portion of segments. All spines with a single point.

Posterior spiracular slits not surrounded by peritreme; long, measuring 120 microns.

Cephalopharyngeal skeleton exceedingly large; length 1.6 mm, width 334 microns; general form (figure 10) similar to that of *S. utilis*. (Drawn to smaller scale.)

Specimens collected at Menard, Texas. Five gravid females, apparently all of this species, produced 5, 5, 7, 7, and 9 larvae. In the case of larvae from two females reared on decaying meats, in one instance one female and in another two females emerged; unfortunately no males emerged, which prevented identification of the species.

Sarcophaga misera var. *sarracenioides* Aldrich

Length of larva 3.3 mm; slightly tapering posteriorly. Anal area small, with a single postero-lateral tubercle on each side of anal opening. Posterior cavity more than one-half the width of the last segment; upper and lower border each with two pairs of tubercles.

Larvae heavily armed with spines. Anterior border of segments 2–10 completely encircled with spines, while on segment 11 the spines are present ventrally and extend well up laterally but are absent dorsally for a short space. Posterior border of segments 6–11 completely encircled with spines; on segment 5 they are present ventrally and usually present dorsally, but absent literally above the lateral fusiform area. The spines are short and broad (figure 69), differing from those of other species so far described; form and color similar on all segments. Dorsal arrangements on segment 5 similar to that in *S. impar* (figure 54); ventral arrangement on segment 8 as in figure 84. Spines rarely with two points. Length of spines on segments 5 and 6, 8 microns. Border of posterior cavity sparsely armed with the usual long hair-like spines. Posterior spiracular slits 60 microns in length; not surrounded by peritreme.

Cephalopharyngeal skeleton of the *utilis* type but much smaller; length 651 microns, width 148 microns.

Specimens collected at Dallas, Texas, by E. W. Laake and by the author at Menard, Texas, Galesburg, Illinois, and Ames, Iowa. Reared on decaying meats. Nine females yielded 14, 21, 30, 34, 39, 48, 50, and 51 larvae. Developmental period, larva to adult, 20 days, May 14 to June 3; 15 days, July 8 to July 23.

Sarcophaga impar Aldrich

Length of larva 3.12 mm. Form as in *S. sarracenioides*. Anal area small, with two laterally directed tubercles, one on each side. Posterior cavity small; transverse diameter approximately one-third as wide as last segment at widest point; upper and lower border each with two pairs of small tubercles, one pair on the lower border poorly defined.

Larva heavily armed; anterior border of segments 2–12 completely encircled with spines; reduced dorsally on segment 12. On segment 11, and more so on 12, the spines at the anterior border are more widely spaced and smaller than on the segments anterior to these. Posterior border of segments 5–12 with complete bands of spines, reduced to one or two rows on segment 5 and to three or four rows on segment 6, the number of rows increasing on each posterior segment. Border of posterior cavity sparsely armed with long hair-like spines. Form of spines, both single and double point, shown in figure 70; similar on all segments. Ventral spines on segment 2 with one to four points; more often only 1, and rarely 3 or 4; spines with two or more points more numerous on anterior border of segments 2 to 5 and on posterior border of segments 10 and 11 than on other regions. Dorsal arrangement of spines on anterior border of segment 5 as in figure 54, ventral arrangement on segment 8 as in figure 85. Length of spines on anterior border of segment 5, 6 microns; of segment 7, 8 microns; on posterior border of segment 11, 10 microns.

Posterior spiracles without peritreme; length of longest slit 44 microns.

Cephalopharyngeal mechanism as in figure 12; length 445 microns, width 110 microns.

Specimens collected at Galesburg, Illinois, and Ames, Iowa. Reared on decaying meats. Five gravid females yielded 11, 19, 22, 26, and 31 larvae. Developmental period, larva to adult, 14 days, July 11 to July 25.

Sarcophaga bullata Parker

Length of larva 2.8 mm. Widest near the middle. Anal area small, with small anal tubercles. Posterior cavity more than one-half width of last segment.

Moderately armed with spines; anterior border of segments 2–9 completely encircled with spines; dorsal spines generally absent on 10. Posterior border of segments 7–12 provided with complete band of spines; on segment 6, spines extend well up laterally but are absent dorsally. Form of spines similar on segments 2–5; beginning on segment 6 the spines are of different type, being lighter in color, longer and narrower near the end, and having a different arrangement in the band. Spines at posterior border of segments are long and slender, resembling those on anterior border of segments 6–10. Length of spines: On anterior border of segment 4, 10 microns, of segment 5, 12 microns; of segment 6, 14 microns; on posterior border of segment 11, 16 microns. Spines on segment 2 rarely with more than one point. Color of lateral and dorsal spines similar on all segments at posterior border;

ventral spines larger and darker in color, except on segments 2–5. Form of spines on segment 5 as in figure 71*a;* on segment 6 as in figure 71*b*. Arrangement of dorsal spines at anterior border of segment 5, and of ventral spines on segment 8 as in figures 55 and 86, respectively.

Spiracular slit 64 microns in length; without peritreme.

Cephalopharyngeal mechanism as in figure 13; length 540 microns, width 120 microns.

Specimens collected at Dallas, Texas, by E. W. Laake, and by the author at Menard, Texas, Galesburg, Illinois, and Ames, Iowa. Reared on decaying meats. Eight gravid females yielded 58, 71, 102, 106, 108, 112, 127, and 140 larvae. On one occasion larvae placed on decomposing meat on May 22 pupated June 1, and adults emerged June 16 or after a period of 25 days.

Sarcophaga barbata Thomson (*falculata* Pandelle)

Length of larva 3.6 mm. Anal area not prominent; two pairs of well defined tubercles directed laterally and posteriorly. Posterior cavity more than one-half width of last segment; two pairs of small tubercles on both upper and lower border.

Moderately armed; segments 2–10 with complete bands of spines on the anterior border; narrowed dorsally on segment 10. Posterior border of segments 7–12 completely encircled with spines; on segment 6, ventral spines and two or three dorsal rows present but absent on lateral surface above lateral fusiform area. The spines vary to the degree of pigment: on segments 2–5 at the anterior border the color is uniform, whereas on segments 6–10 the spines are more lightly pigmented laterally and dorsally, becoming lighter posteriorly on each segment, while the ventral spines are of the same color on all segments and as heavily pigmented as on segments 2–5. At the posterior border of the segments the spines become darker on each posterior segment and are almost as dark laterally and dorsally as ventrally on segments 10 and 11. Posterior border of segment 12 not heavily armed. As in *S. bullata,* the anterior border spines on segments 2–5 do not resemble in form the spines on the following segments (figures 72*a* and 72*b*); in *S. barbata* the difference is even more pronounced. The spines located on the posterior border of the segments have the same general form as those at the anterior border of segments 6–10 (figure 72*c*). Arrangement of spines on segment 5 and on ventral sides of segment 8 as in figures 57 and 88, respectively. Ventral spines on segment 2 occasionally with two and rarely with three points. Length of spines: On anterior border of segment 4, 10 microns; of segment 5, 12 microns; of segment 6, 18 microns; on posterior border of segment 11, 20 microns.

Posterior spiracles without ring surrounding the spiracular slits; length 62 microns.

Cephalopharyngeal mechanism as in figure 14; length 595 microns, width 140 microns.

Specimens collected at Dallas, Texas, by E. W. Laake and by the author at Ames, Iowa. Reared on decaying meats. Approximately 60 larvae collected from one gravid female.

Sarcophaga securifera Villeneuve

Similar to *S. barbata*; the anterior border of segments 2–11 provided with a complete band of spines, whereas in *S. barbata* the dorsal spines are absent on segment 11 and very sparse on segment 10. Segments 6–12 at posterior border completely encircled with spines. In general the spines are longer, darker, and narrower in *S. securifera* (figure 73). Spines with two and three points more numerous on segment 2 than in *S. barbata.*

Smith (10) has figured the cephalopharyngeal skeleton; it is similar to that of *S. barbata,* but differs slightly in the curvature of the oral hooks, and is less rounded on the outer edge. Cephalopharyngeal skeletons show differences in size; the measurements of an average of eight larvae of each species are as follows: Length from tip of oral hooks to posterior extremity of dorsal cornu, *securifera* 595 microns, *barbata* 580 microns; width, 148 and 133 microns, respectively; length of oral hooks from tip to posterior edge of basal portion, 189 and 173 microns, respectively.

Collected at Washington, D. C., by C. N. Smith.

Sarcophaga plinthopyga Wiedemann

(*robusta* Aldrich)

Resembling *S. barbata* and *S. securifera* in general form of body.

Anterior border of segments 2–5 with dark conspicuous spines, equally as dark dorsally and laterally as they are ventrally; beginning on segment 6 the dorsal and lateral spines are almost without pigment, and on superficial examination appear to be absent; they completely encircle segments 6–9 as well as 2–5. Posterior border of segments 9–11 with a completely encircling band of spines; segment 9 with several rows of long lightly colored dorsal spines; on segments 10 and 11 the spines as dark as those on segments 2–5 and those on ventral surface of segments 6–12. Form of spines at anterior border of segment 5 and 6 and posterior border of segment 11 shown in figures 74*a, b,* and *c,* respectively. It will be noted that the spines at the posterior border of segment 11 resembles more closely those at the anterior border of segment 5; whereas in *S. bullata, S. barbata,* and *S. securifera* the spines

at the posterior border of the segments are of the same type as those at the anterior border of segment 6 and the following. Figure 56 shows the arrangement of spines on segment 5; figure 87 shows the ventral arrangement on segment 8. Ventral spines on segment 2 generally with one point, but occasionally with two points.

Length of spines: On anterior border of segment 5, 14 microns; of segment 6, 18 microns; on posterior border of segment 11, 14 microns.

Posterior spiracles as shown in figure 26; length 72 microns.

Cephalopharyngeal mechanism as in figure 15; length 576 microns, width 132 microns.

Collected at Dallas, Texas, by E. W. Laake, and also by the author at Menard, Texas. Reared on decaying meats. Three females yielded 34, 36, and 40 larvae, respectively.

Sarcophaga kellyi Aldrich

Length 2.7 mm. Anal area small, with poorly defined lateral tubercles. Posterior cavity approximately one-half width of last segment; upper and lower borders each with two pairs of small tubercles; inner pair on lower border small and inconspicuous.

Not heavily armed; anterior border of segments 2–7 provided with a complete band of spines; reduced to one or two dorsal rows on segment 7. Spines on segments 3–5 similar; narrowed and more lightly pigmented on dorsum of segments 6 and 7. Posterior border of segments 9–11 provided with a complete band of spines; prominent on segments 10 and 11 but poorly defined dorsally on 9. Spines absent at posterior border of last segment. Arrangement of spines on segment 5 and on ventral region of segment 8 as in figures 58 and 89, respectively. Spines small (figure 75), similar in form on segments 2–5. On segments 2, ventrally, the spines more often than not with two points; with a single point on other segments. Length of spines: On segment 4, 8 microns; on segment 6, 6 microns; on posterior border of segment 11, 12 microns.

Posterior spiracular slits measuring 44 microns. Upper end of slits provided with a spine-like point, which is lighter in color and not easily noted except on close examination.

Collected at Dallas, Texas, by E. W. Laake and at Ames, Iowa, by the writer. Reared on decayed meats. One gravid female produced 34 larvae. Developmental period, larva to adult, 16 days, May 25 to June 9.

Sarcophaga rapax Walker

(*helicis* Townsend)

A small species; length of newly deposited larva 2.5 mm.; slender, as in figure 43. Anal area small. Posterior cavity small, with two pairs of small papillae each on upper and lower borders.

Not heavily armed; spines at anterior border completely encircling segments 2–9; reduced dorsally on 9. Posterior border of segments 9–11 with complete ring of spines. There are two types of spines; on segments 2–5 they are of the type shown in figure 76; on lateral and dorsal surfaces of segments 6–12 they resemble the single-point spines of *S. cimbicis,* (figure 77*a*). Spines dark on segments 2–5; on segments 6 and those following, at both anterior and posterior borders; lateral and dorsal spines are lightly pigmented, but the ventral darker. Border of posterior cavity lightly armed with spines. Arrangement of spines on segment 5 and on ventral area on segment 8 shown in figures 59 and 90, respectively. One and two point ventral spines on segment 2; single-point spines on all other segments. Length of spines: On segment 5, 6 microns; on segment 6, 14 microns.

Posterior spiracular slits short and comparatively broad; length 26 microns.

Cephalopharyngeal mechanism small (figure 17), length 427 microns.

Collected at Dallas, Texas, by E. W. Laake and by the author at Menard, Texas and Ames, Iowa. One gravid female produced 31 larvae. Developmental period, larva to adult, on decaying meat, 12 days, May 23 to June 4.

Sarcophaga latisterna Parker

Length of larva 3mm. Tapering anteriorly from about the middle, slightly tapering posteriorly (figure 44). Anal area small, with a pair of small, well defined tubercles directed laterally and posteriorly.

Well armed with spines; a complete band of spines at anterior border of segments extending to segment 11. Posterior border of segments 9–12 always completely encircled with bands of spines; segment 8 more often than not provided with a complete band but greatly reduced or absent entirely on dorsal surface. Color of dorsal and lateral spines similar on all segments. Spines longer and with much darker pigment on ventral surface of segments 5–9, especially in the posterior rows of each segment (figures 44 and 91). General arrangement of spines on segment 5 shown in figure 60; similar on other segments. The spines of this and the following species, *S. cimbicis,* differ greatly from those of other species studied; they are long and slender on all of segments 3 and 4 and on lateral and dorsal regions of other segments; generally with a single point in these regions, but occasionally with double point, figures 77*a* and 77*b*. Ventrally, on segments 5–9, the spines appear as in figure 91. The number of points may range from 1 to 8 or more, the posterior rows of ventral spines having the most points; a single spine from the posterior rows, more enlarged, as shown in figure 77*c*. On segment 10 the ventral spines becomes smaller and lighter in color,

and fewer of them possess multiple points. Segment 2 with shorter but larger spines than those on segments 3 and 4; spines with one to three points, more often with two and three on ventral half. Length of spines: On segment 5, 16 microns; on segment 7, 20 microns; on posterior border of segment 11, 28 microns; the largest ventral spines on segments 5–9 measure 30–40 microns.

Posterior spiracular slits 52 microns in length. Cephalopharyngeal mechanism as in figure 19; length 650 microns, width 123 microns, length of oral hooks 232 microns.

Larvae collected at Galesburg, Illinois. Reared on decomposing hamburger meat.

Sarcophaga cimbicis Townsend (*setulosa* v. d. Wulp)

So similar to *S. latisterna* that only the differences will be mentioned. Ventral spines on segment 5 divided by a small but distinct transverse spineless area, and on segment 6 the transverse spineless area nearly as large as on segment 7, whereas in *latisterna* the ventral spines not distinctly divided by a transverse spineless area, and on the sixth segment this area much smaller than on the seventh.

The cephalopharyngeal mechanism (figure 18) of the same type as that of *S. latisterna* but smaller; comparative measurements as follows: Total length, *cimbicis,* 632, *latisterna,* 650 microns; width, *cimbicis,* 126, *latisterna,* 128 microns; length of oral hooks from tip to posterior edge of basal portion, *cimbicis,* 232, *latisterna,* 272 microns.

Posterior spiracular slits 72 microns in length.

Collected at Galesburg, Illinois. Reared on decomposing hamburger meat. Twenty-one larvae collected from one female. Developmental period, 21 days, May 16 to June 6.

Sarcophaga "A". Prohibita Group.

Length 1.5 mm. General form as shown in figure 45. Anal area with rather prominent tubercles directed posteriorly and laterally.

Heavily armed with long dark spines on ventral region; dorsal portion lightly armed with small lighter spines. Anterior border of segment 2 provided with several rows of large conspicuous spines; on 3 the spines are small and lightly pigmented and on segment 4 the spines are long and dark, extending well up to the dorsal surface, where they abruptly become smaller and almost colorless and appear to be absent except on close examination. On segments 5 and 6 the spines are slightly longer but do not extend as far dorsally as on segments 3 and 4; on the seventh and following segments the longer and darker spines do not extend above the lateral surface, although the smaller almost colorless spines may extend almost to the dorsal surface. A ventral transverse spineless area

present on segments 6–12. Length of longest spines on segment 4, 28 mm: On segment 5, 36 mm; on segment 6, 48 mm. In addition to the larger spines there are others, long, slender, and hair-like, located laterally on each segment beginning with the second; they may measure as much as 24 microns in length, but they are so slender and lightly pigmented in contrast with the larger spines that they are not readily noticed.

Posterior spiracles resembling those of *Sarcophaga "B"* (figure 27).

Cephalopharyngeal mechanism as in figure 20. (Drawn to larger scale.) Length 280 microns.

Collected at Galesburg, Illinois. Attempts to rear the larva of this and another closely related species on decaying meat and on cow manure were unsuccessful. One female produced 43 larvae. The larvae are very active and crawl rapidly when squeezed from the abdomen of the female.

Sarcophaga "B". Prohibita Group

Small larvae. Length at time of hatching 1.5 mm. Widest near the middle, tapering posteriorly and anteriorly (figure 46).

Heavily armed with peculiarly developed spines; anterior border of segments 2–8 provided with spines that completely encircle the body; restricted ventrally and laterally on segments 9–12. Spines at anterior border small, almost invisible near posterior border of band. Posterior border of segments with long, well developed, anteriorly directed spines on segments 5–11 inclusive. Spines restricted to the ventral and lateral surfaces on this region of the segments; much longer laterally than ventrally, absent dorsally. Length of longest lateral spines on segment 6, 120 microns; of ventral spines on same segment, 20 mm. Although the larvae were not noted in action, no doubt this species would move with the posterior end foremost, as in Sarcophaga *"C"*, for the long anteriorly directed spines probably would hinder movement in the usual direction. This and the following species are the only ones studied in which the spines at the posterior border of the segments are more highly developed than those at the anterior margins of the segments.

Posterior spiracles, as in the preceding species, of unusual type (figure 27).

Cephalopharyngeal mechanism shown in figure 21. Length approximately 300 microns. (Drawn to larger scale.)

Sarcophaga "C". Prohibita Group.

Form similar to above. (Not figured.) Length of larva 2 mm. Moderately armed with spines. As in *Sarcophaga "B"*, the spines at the posterior border of the segments are more highly developed than at the anterior border, but much smaller, the longest spine at the posterior

border of segment 8 measuring 10 microns in length; spines at anterior border minute.

Posterior spiracles similar to those of *Sarcophaga "B"*.

The cephalopharyngeal mechanism shows peculiar development (lateral view in figure 22). Ventral view of same in figure 23 (note position of oral hooks as compared with the position in the other species).

Only 12 larvae were collected from a gravid female fly and attempts to rear them on *Hypoderma* pupae were without success. The larvae are very active and when released near the opening made in the *Hypoderma* pupal case they immediately began crawling rapidly into the opening, with the posterior end in the direction of travel. Efforts to induce movement in usual manner (i.e., anterior end in the direction of travel) proved unsuccessful.

References

(1) Aldrich, J. M. 1916.—Sarcophaga and allies in North America. 301 pp., illus., Lafayette, Ind.

(2) Banks, N. 1912.—The structure of certain dipterous larvae with particular reference to those in human foods. U. S. Dept. Agr., Bur. Ent. Tech. Ser. (Bull.) 22, 44 pp., illus.

(3) Greene, C. T. 1925.—The puparia and larvae of sarcophagid flies. Proc. U. S. Nat. Mus. 66, art. 29: 1–26, illus.

(4) Hall, D. G. 1929.—An annotated list of the Sarcophaginae which have been collected in Kansas. Jour. Kansas Ent. Soc. 2: 83–90.

(5) 1932.—Biology of *Sarothromyia femoralis* var. *simplex* Aldrich. (Diptera, Calliphoridae.) Ann. Ent. Soc. Amer. 25: 641–647, illus.

(6) Keilin, D. 1924.—On a case of intestinal myiasis in man produced by the larvae of a sarcophagine fly. Parasitology 16: 318–320, illus.

(7) Moutia, A. 1930.—Flies injurious to domestic animals in Mauritius. Dept. Agr. Mauritius, Sci. Ser. Bull. 15, 8 pp., illus.

(8) Patton, W. S., and Evans A. M. 1929.—Insects, ticks, mites and venomous animals. Part I.—Medical. 786 pp., illus. Croydon.

(9) Root, F. M. 1923.—Notes on larval characters in the genus Sarcophaga. Jour. Parasitology 9: 227–229, illus.

(10) Smith, C. N. 1933.—Notes on the life history and molting process of *Sarcophaga securifera* Villeneuve. Proc. Ent. Soc. Wash. 35: 159–164, illus.

(11) Tao, S. M. 1927.—A comparative study of the early larval stages of some common flies. Amer. Jour. Hygiene 7: 735–761, illus.

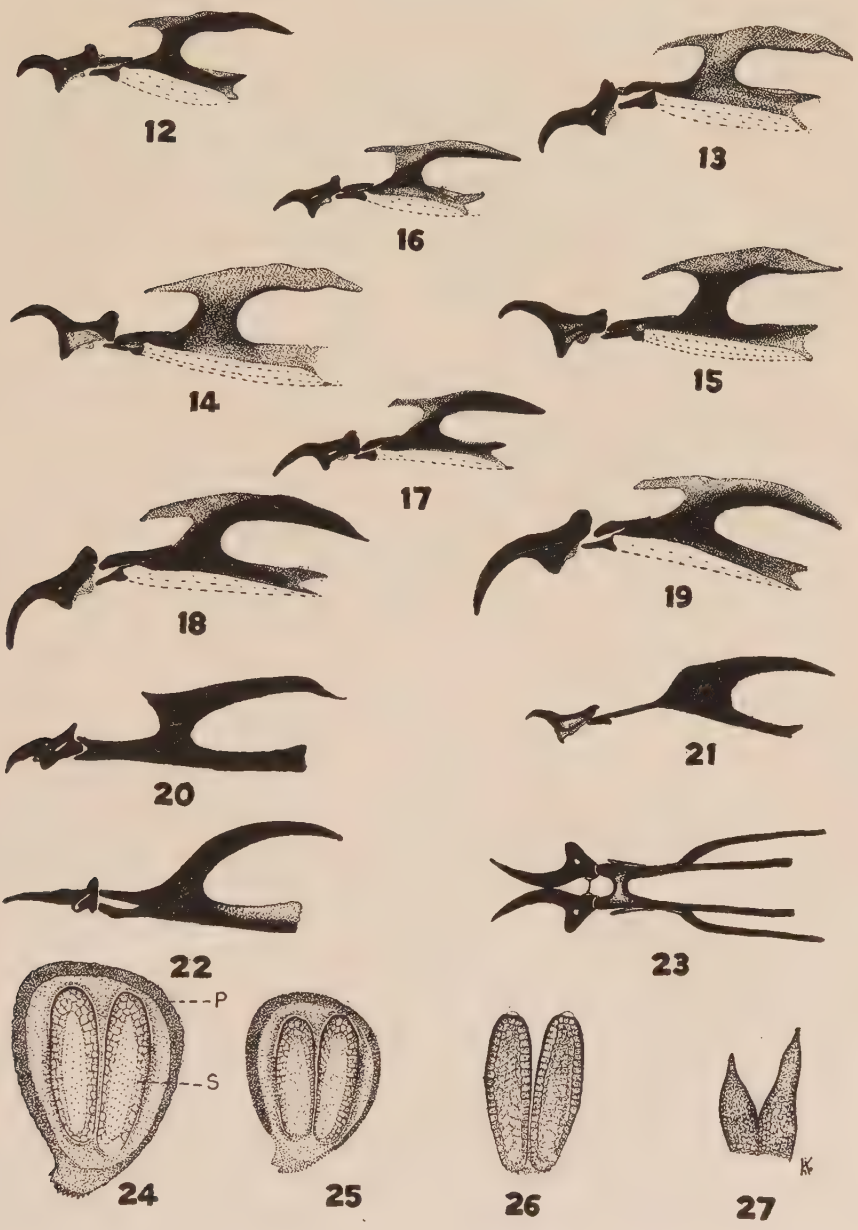
Plates I and II

Figures 1–22 show lateral view of cephalopharyngeal mechanism. Figure 10 enlarged ×70; figures 1–9 and 11–19, ×85; figure 20, ×175; figure 21, ×140; figure 22, × 150.

Fig. 1. *Sarcophaga galeata* Aldrich. *OH,* oral hooks; *HS,* hypostomal sclerites; *DPS,* dorso-pharyngeal sclerite; *PHS,* pharyngeal sclerite; *PH,* pharynx; *VC,* ventral cornu; *DC,* dorsal cornu.
Fig. 2. *Sarcophaga ventricosa* v. d. Wulp.
Fig. 3. *Sarcophaga pusiola* v. d. Wulp.
Fig. 4. *Sarcophaga stimulans* Walker.
Fig. 5. *Sarcophaga laakei* Hall.
Fig. 6. *Sarcophaga lherminieri* Robineau-Desvoidy.
Fig. 7. *Sarcophaga sueta* v. d. Wulp.
Fig. 8. *Sarcophaga haemorrhoidalis* Fallen.
Fig. 9. *Sarcophaga utilis* Aldrich.
Fig. 10. *Sarcophaga* sp.
Fig. 11. *Sarcophaga misera* var. *sarracenioides* Aldrich.
Fig. 12. *Sarcophaga impar* Aldrich.
Fig. 13. *Sarcophaga bullata* Parker.
Fig. 14. *Sarcophaga barbata* Thomson.
Fig. 15. *Sarcophaga plinthopyga* Wiedemann.
Fig. 16. *Sarcophaga kellyi* Aldrich.
Fig. 17. *Sarcophaga rapax* Walker.
Fig. 18. *Sarcophaga latisterna* Parker.
Fig. 19. *Sarcophaga cimbicis* Townsend.
Fig. 20. *Sarcophaga "A".*
Fig. 21. *Sarcophaga "B".*
Fig. 22. *Sarcophaga "C".*
Fig. 23. Same as figure 22, showing ventral view of cephalopharyngeal mechanism.
Fig. 24. *Sarcophaga galeata* Aldrich, showing right spiracular plate, ×280. *P,* peritreme; *S,* spiracular slit.
Fig. 25. *Sarcophaga ventricosa* v. d. Wulp, same as figure 24.
Fig. 26. *Sarcophaga plinthopyga* Wiedemann, same as figure 24, ×300.
Fig. 27. *Sarcophaga "B",* same as figure 24, ×585.

PLATE I

PLATE II



Plates III and IV

Lateral view of first-instar larvae when fully relaxed. Figures 28–44, approximately ×25; figures 45 and 46, ×44. Distribution of spines partly diagrammatic.

Fig. 28. *Sarcophaga galeata* Aldrich. *PO,* photoreceptive organs; *OB,* oral band; *LF,* lateral fusiform area; *VF,* ventral fusiform area; *AS,* spines at anterior border of segment; *PS,* spines at posterior border of segment; *PC,* posterior cavity; *T,* tubercle on border of posterior cavity; *A,* anal area; *PT,* posteriorly directed tubercle on anal area; *LT,* laterally directed tubercle on anal area; *X* indicates the approximate portions of spinose band enlarged in figures 47–60, Plate V; *Y* shows portion of ventral spines enlarged in figures 78–91.
Fig. 29. *Sarcophaga ventricosa* v. d. Wulp.
Fig. 30. *Sarcophaga pusiola* v. d. Wulp.
Fig. 31. *Sarcophaga stimulans* Walker.
Fig. 32. *Sarcophaga laakei* Hall.
Fig. 33. *Sarcophaga sueta* v. d. Wulp.
Fig. 34. *Sarcophaga lherminier*i Robineau-Desvoidy.
Fig. 35. *Sarcophaga haemorrhoidalis* Fallen.
Fig. 36. *Sarcophaga utilis* Aldrich.
Fig. 37. *Sarcophaga misera* var. *sarracenioides* Aldrich.
Fig. 38. *Sarcophaga impar* Aldrich.
Fig. 39. *Sarcophaga bullata* Parker.
Fig. 40. *Sarcophaga barbata* Thomson.
Fig. 41. *Sarcophaga plinthopyga* Wiedemann.
Fig. 42. *Sarcophaga kellyi* Aldrich.
Fig. 43. *Sarcophaga rapax* Walker.
Fig. 44. *Sarcophaga latisterna* Parker.
Fig. 45. *Sarcophaga "A".*
Fig. 46. *Sarcophaga "B".*

Plate V

Figures 47–60 show arrangement of spines in band on anterior margin of segment. Only a short section of the band is shown, as delineated by *X,* in figure 28, Plate III. Figures 51 and 52 were made from segment 6; all others from segment 5. All figures are greatly enlarged and roughly drawn to the same scale.

Fig. 47. *Sarcophaga galeata* Aldrich.
Fig. 48. *Sarcophaga australis* Aldrich.
Fig. 49. *Sarcophaga pusiola* v. d. Wulp.
Fig. 50. *Sarcophaga laakei* Hall.
Fig. 51. *Sarcophaga lherminieri* Robineau-Desvoidy.
Fig. 52. *Sarcophaga sueta* v. d. Wulp.
Fig. 53. *Sarcophaga utilis* Aldrich.
Fig. 54. *Sarcophaga impar* Aldrich.
Fig. 55. *Sarcophaga bullata* Parker.
Fig. 56. *Sarcophaga plinthopyga* Wiedemann.
Fig. 57. *Sarcophaga barbata* Thomson.
Fig. 58. *Sarcophaga kellyi* Aldrich.
Fig. 59. *Sarcophaga rapax* Walker.
Fig. 60. *Sarcophaga cimbicis* Townsend.

Figures 61–77 show spines enlarged. With the exception of figures 77*c,* the spines figured are those near the dorsal surface and are representative of the

PLATE III

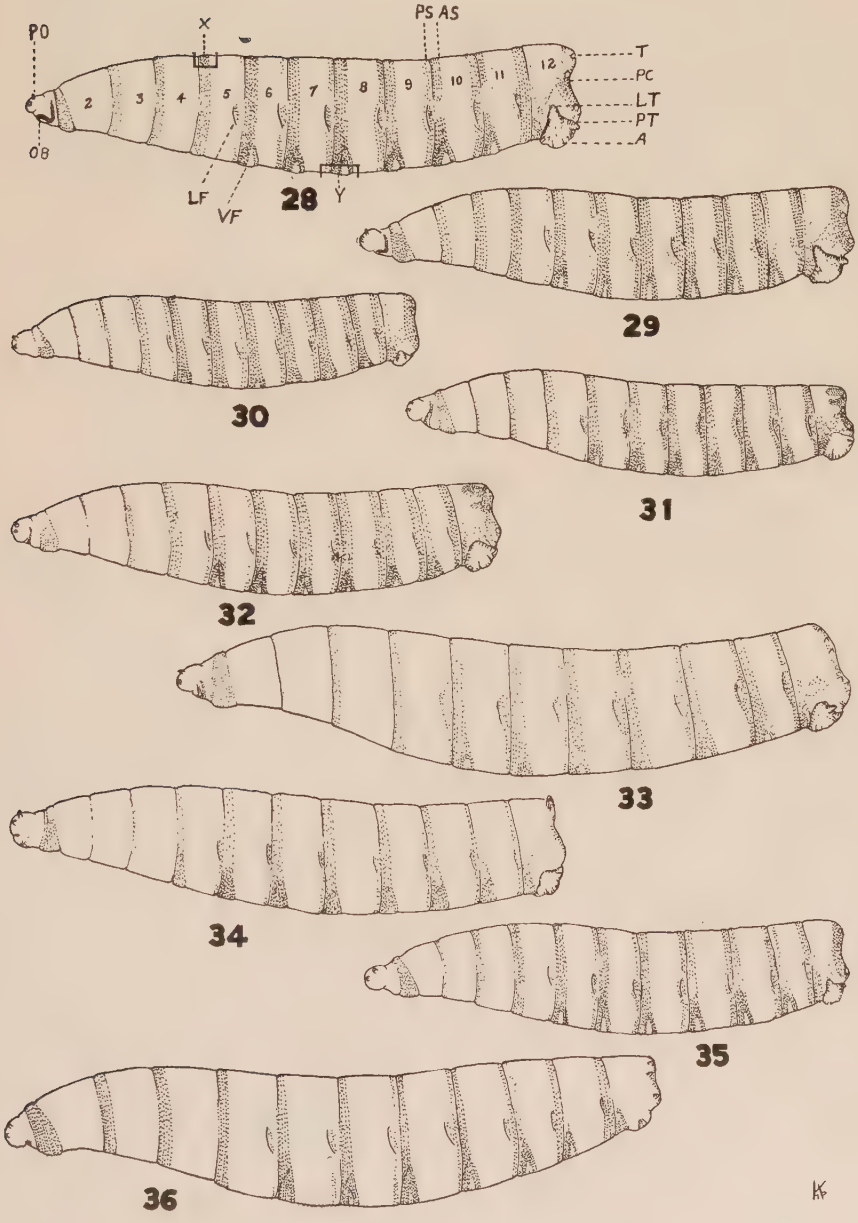
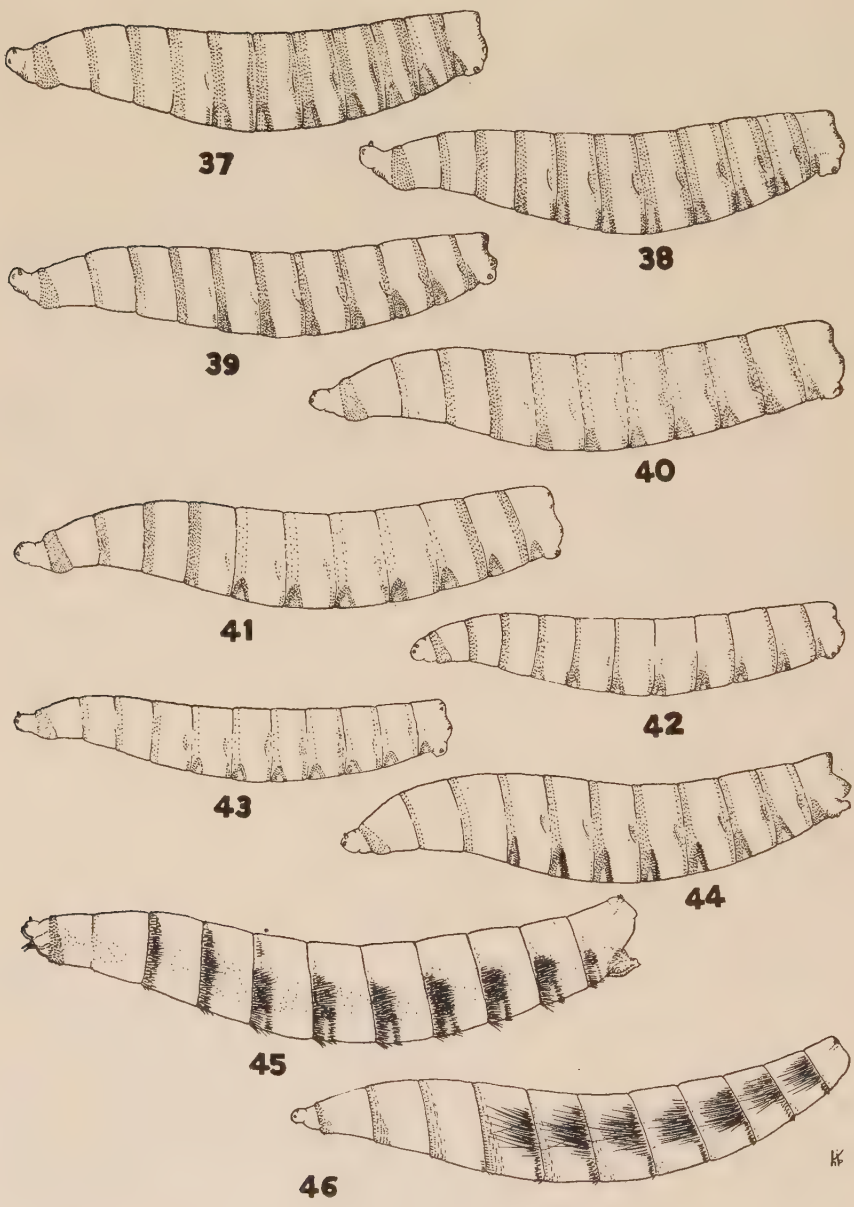

PO
X
PS AS
T
PC
LT
PT
A
OB
2
3
4
5
6
7
8
9
10
11
12
LF
VF
Y
28
29
30
31
32
33
34
35
36

PLATE IV



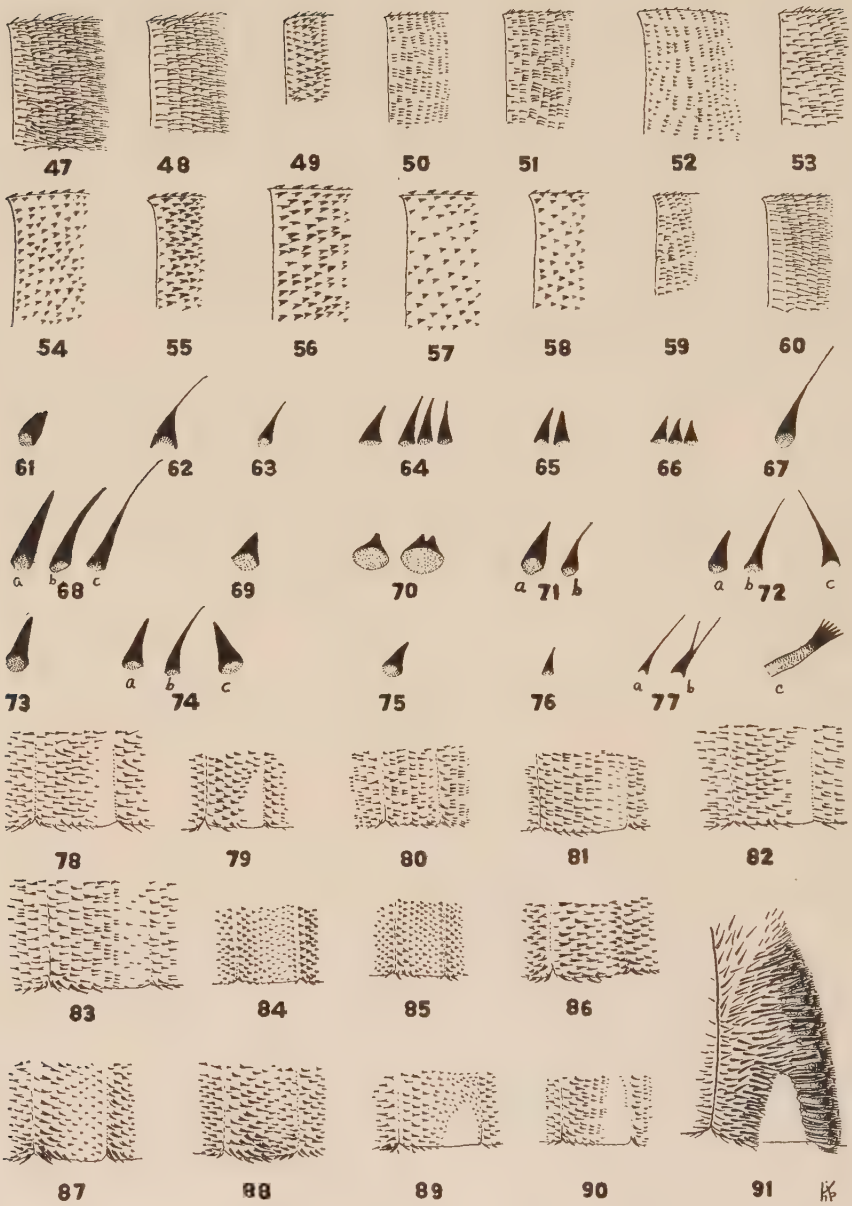
larger spines in this region. Figure 77*c* shows the appearance of one of the larger spines from the ventral region of the larva. Enlarged ×750.

FIG. 61. *Sarcophaga galeata* Aldrich. From anterior border of segment 6.
FIG. 62. *Sarcophaga pusiola* v. d. Wulp. From anterior border of segment 6.
FIG. 63. *Sarcophaga stimulans* Walker. From anterior border of segment 6.
FIG. 64. *Sarcophaga laakei* Hall. From anterior border of segment 6.
FIG. 65. *Sarcophaga lherminieri* Robineau-Desvoidy. From anterior border of segment 6.
FIG. 66. *Sarcophaga sueta* v. d. Wulp. From anterior border of segment 6.
FIG. 67. *Sarcophaga haemorrhoidalis* Fallen. From anterior border of segment 6.
FIG. 68. *Sarcophaga utilis* Aldrich. *a, b,* and *c,* from anterior border of segments 4, 5, and 6, respectively.
FIG. 69. *Sarcophaga misera* var. *sarracenioides* Aldrich. From anterior border of segment 6.
FIG. 70. *Sarcophaga impar* Aldrich. From anterior border of segment 6, showing single and double point spines.
FIG. 71. *Sarcophaga bullata* Parker. *a,* From anterior border of segment 5; *b,* from same of segment 6.
FIG. 72. *Sarcophaga barbata* Thomson. *a* and *b,* From anterior border of segments 5 and 6, respectively; *c,* From posterior border of segment 11.
FIG. 73. *Sarcophaga securifera* Villeneuve. From anterior border of segment 5.
FIG. 74. *Sarcophaga plinthopyga* Wiedemann. *a* and *b,* From anterior border of segments 5 and 6, respectively; *c,* From posterior border of segment 11.
FIG. 75. *Sarcophaga kellyi* Aldrich. From anterior border of segment 5.
FIG. 76. *Sarcophaga rapax* Walker. From anterior border of segment 5.
FIG. 77. *Sarcophaga cimbicis* Townsend. *a* and *b,* From anterior border of segment 6; *c,* Ventrally on segment 8.

Figures 78–91 represent a ventral to ventro-lateral view of the spinose area on segment 8 of a number of the species. (See *Y,* figure 28, Plate III.) Not accurately drawn to scale. Figure 91, more enlarged and showing a larger portion of the ventral area.

FIG. 78. *Sarcophaga galeata* Aldrich.
FIG. 79. *Sarcophaga pusiola* v. d. Wulp.
FIG. 80. *Sarcophaga laakei* Hall.
FIG. 81. *Sarcophaga lherminieri* Robineau-Desvoidy.
FIG. 82. *Sarcophaga haemorrhoidalis* Fallen.
FIG. 83. *Sarcophaga utilis* Aldrich.
FIG. 84. *Sarcophaga misera* var. *sarracenioides* Aldrich.
FIG. 85. *Sarcophaga impar* Aldrich.
FIG. 86. *Sarcophaga bullata* Parker.
FIG. 87. *Sarcophaga plinthopyga* Wiedemann.
FIG. 88. *Sarcophaga barbata* Thomson.
FIG. 89. *Sarcophaga kellyi* Aldrich.
FIG. 90. *Sarcophaga rapax* Walker.
FIG. 91. *Sarcophaga cimbicis* Townsend.

PLATE V


47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65
66
67
a
b
c
68
69
70
a
71
b
a
b
72
c
73
a
b
74
c
75
76
a
77
b
c
78
79
80
81
82
83
84
85
86
87
88
89
90
91

EXPERIMENTAL STUDIES OF FACTORS INFLUENCING THE DEVELOPMENT OF THE EGGS OF PIG ASCARID (*ASCARIS SUUM* GOEZE)[1]

GEORGE C. HUFF

I. SIGNIFICANCE OF THE ALBUMINOUS COATING AT 38° C.

Since the work of Davaine (1863), who found that the ova of *Ascaris lumbricoides* remained infective after storage for five years, and of Baillet (1866), who observed that the eggs of *A. suum* remained viable after twelve months' exposure to the heat of summer and to the cold of winter, a voluminous literature has accumulated regarding the influences of various factors on the development of the eggs of ascarids.

The effect of various temperatures on development has been studied by Fauré-Fremiet (1913), who showed that the ova of *A. suum* are capable of development at varying temperatures below 35° C., but that the optimum temperature is about 30°. Wharton (1915), determined that at temperatures around 37° C. ova of *Ascaris lumbricoides* developed to the eight-cell stage and then died.

As reported by Nolf (1932), the ova of human ascaris are more resistant to the effects of high temperature exposure than those of trichuris, as shown by the fact that 68% of ascaris ova eventually became embryonated following exposure for three minutes at 53° C., whereas no trichuris ova survived similar treatment. Ogata (1925), studied the effect of heat in the destruction of the ova of *Ascaris lumbricoides* and found that no eggs developed following exposure to 70° C. for one minute, and that they were unaffected by exposure to temperatures up to 45° C. for a period of one hour.

Despite the fact that so much has been done on the effect of temperature, many of the results, especially at the lower lethal level and at the maximum temperature for continuous development, are not complete nor in agreement, and the mechanism of the resistance to both cold and heat is little understood.

It was thought that the presence or absence of the albuminous coating, so characteristic of the eggs of ascarids, might play some part in controlling the influence of such physical factors as heat and cold, and the experiments to be described were designed to demonstrate the effect of removal of the coating on the response to high temperature.

---

[1] From the Zoological Laboratories of the State University of Iowa. The writer wishes to acknowledge the valuable advice and helpful criticism of Dr. L. O. Nolf.

MATERIALS AND METHODS

Living adult specimens of the pig ascarid (*Ascaris suum* Goeze), removed from the intestines of freshly killed pigs, were opened, the uterus pulled out and cut free at a point about one and one-half inches from the vagina, and the eggs from more than 100 worms expressed into a 1 : 1000 formalin solution. Approximately one-half of these ova were mixed with ten per cent antiformin and examined miscroscopically. As soon as the albuminous covering seemed to have been dissolved from about three-fourths of the ova, they were flooded with water, and the antiformin removed by washing and centrifugation through seven or eight changes of water. By the time this washing process had been completed, ninety-eight per cent of the eggs showed no remaining traces of the albumin. Two lots of eggs were obtained by this treatment; one group with albumin intact, the other with the albuminous coating removed. Both kinds of eggs in 1 : 1000 formalin were stored in the refrigerator at 8°–12° C. until needed for the experiments.

The ova were cultured in Petri dishes with porous lids, the bottoms of which were lined with moist cellucotton to prevent desiccation. In preparation for the experiments, the eggs were flooded over glass slides and allowed to dry in the air after which the slides were placed in the culture chambers for incubation at the desired temperature. The Petri dishes thus prepared were then incubated at the desired temperature in a $6'' \times 8'' \times 6''$ closed box immersed in a large water bath and ventilated by a $\frac{1}{4}''$ bore glass tube which protuded above the surface of the bath. The incubator chamber showed temperature fluctuations of no more than $\pm .25°$ C. The use of such chambers for culturing made possible the maintenance of a saturated atmosphere during the course of the experiment and prevented water of condensation from accumulating over the eggs, so that although the ova were moist at all times, they were not immersed in water.

The progress of development was followed and recorded daily according to the method of Brown (1928). The developing eggs were classified and the various stages assigned index numbers as follows: 1 cell, 0; 2–16 cell to complete morula, 2; incurved morula to early vermiform, 3; motile embryo, 4. In practice the slides were removed from the culture chambers, a small area moistened, and the percentage of eggs in various stages of development determined by actual observation of at least three hundred eggs. The percentage of ova in each stage was then multiplied by the index number for that stage and the results totaled, giving an index number representative of the developmental picture at the time of observation. Thus if 33% of the ova were in the morula and 67% in the incurved morula stages, the index number would be (2×33) plus (3×67) or 267. This method allows

for the variation in rate of development which is usually apparent in ascaris cultures.

Special methods used in the various phases of the investigations will be described in connection with the procedures to which they apply.

EXPERIMENTS AND RESULTS

To determine the significance of the albuminous coating at optimum temperature, a number of culture chambers containing eggs from which the albumin had been removed were placed in the water bath incubator at 30° C. and the development of the ova compared with that of controls in similar chambers at the same temperature but with the albuminous coating intact.

The effect of removal of the albumin upon development at higher temperatures was studied by incubating treated and untreated ova in additional culture chambers at a constant temperature of 38° C.

In Table 1 the index number given for each day of development is the average of nine experiments performed at different times and using different batches of eggs. Each index number is representative of at

TABLE 1.—*Index number of stage of development of ova of A. suum by days*

Days	1	2	3	4	5	6	7	8	9	10	11
30° C. With Albumin ..	0	64	91	155	186	204	264	309	371	389	391
30° C. Without Albumin	0	63	79	120	187	210	256	308	361	380	387
38° C. With Albumin ..	45	72	83	88	92	94	94	94			
38° C. Without Albumin	51	80	87	100	119	132	148	157	180	258	284

least 2700 ova. The eggs that developed at 30° C., both with and without albumin showed no significant variations and the index numbers corresponded very closely with those given for similar conditions by Brown (1928). The data of Table 1 are presented graphically in Figure 1.

The development of treated and untreated ova kept continuously at a temperature of 38° C. showed marked variation. Initially there was an acceleration, for 50% of the eggs of both groups had divided by the end of the first day, but cell divisions were markedly retarded after the second day not only in the treated eggs but in the untreated ones as well.

Divisions in the eggs with the albumin coating continued very slowly until the fifth day at which time 92% were in the 8–16 cell stage, after which there was no further development. By the end of the third day all of these ova had developed a large vacuole inside the shell which increased very slightly in size. At the close of the ninth day 85% of the eggs showed large vacuolations in the protoplasm and by the end

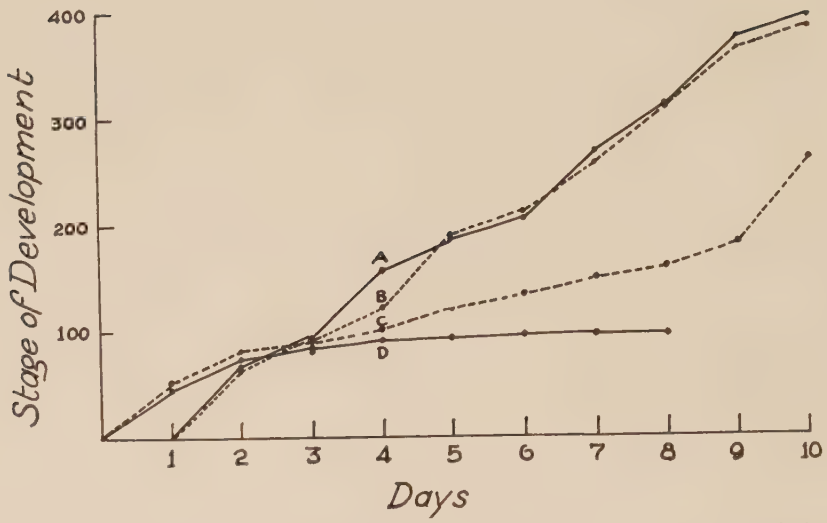


FIG. 1. Morphological development of ova of *A. suum*. Ordinates, index number of development. Abscissae, time in days. Curve A, ova with albumin at 30° C. Curve B, ova without albumin at 30° C. Curve C, ova without albumin at 38° C. Curve D, ova with albumin at 38° C. Data from Table I.

of the twelfth day 68% of the eggs showed complete disorganization of the protoplasm. After the fifth day many of the eggs from which the albumin had been removed seemed to overcome the retarding factor, for they showed from that time on a rate which was about the same as that of untreated ova kept at 30° C. Not only did many of these treated eggs develop through the tadpole stage, but 11% actually became embryonated at 38° C.

II. THE ALBUMINOUS COATING AND GASEOUS EXCHANGE IN DEVELOPING OVA.

Studies of the influence of oxygen on developing ascarid ova have been made by numerous investigators. That oxygen is necessary for growth has been demonstrated by Zavadovskii (1916) and others. Brown (1928), using the Winkler technique, determined the amount of O_2 necessary for the development of eggs of *A. suum,* and found the ova to be capable of development at reduced partial pressures and that the rate could not be accelerated by increased partial pressures of oxygen nor by increased oxygen pressure. The method used, however, permitted determinations only at relatively infrequent intervals and there was no practical possibility of renewing the supply of gas during the course of the experiment.

The experiments described in the first part of this paper indicate that the albuminous coating of the ova of *A. suum* may play some

important part in their development in relation to temperature. Bodine (1929), Inman (1921), and others have shown that injuries to cells are very quickly reflected in changes in the rate of respiration, and it was thought that if respiration could be continuously studied throughout the developmental period of ascaris ova, oxygen consumption might be used as a measure of the physiological affects of various factors, such as removal of the albumin, which are known to influence the eggs during development.

MATERIALS AND METHODS

The respiratory exchange of gases was measured by means of Krogh microdifferential respirometers, using the techniques and calibration formulae described by Dixon (1934), with only such modifications as were necessary to adapt the instruments to the characteristics of the material used. The gas determinations were made with the respirometers in a water bath the temperature of which was $30° \pm .05°$ C. In the early experiments it was found that when ova were placed in small glass cups designed to contain them during the course of the measurements, the eggs settled to the bottom of the drop of water so that development at the bottom of the pile was much slower than at the top. A cup was then designed which could be suspended "cup-side-down" in the respirometer flask. In the experiments, a drop of water containing ca. 500 to 1100 ova was placed in the concavity of the cup, and the cup inverted. The eggs gravitated to the periphery of the hanging drop thus formed and arranged themselves in a thin layer at the surface, each egg with approximately equal exposure to the surrounding gas mixture. This hanging drop method facilitated counting, for at the end of any desired period, the cup was lifted out, and the drop touched lightly to a squared slide, whereupon nearly all ova were transferred to the slide for subsequent counting and microscopical examination. The few ova adhering to the cup could easily be counted by observation with a low power objective.

No single group of eggs was allowed to remain in a respirometer for longer than three days. This necessitated the preparation of a series of culture chambers in which reserve ova were stored in hanging drops in the water bath until needed for transfer to the cups for the actual gas change determinations. The rate of development in these reserve chambers was indistinguishable morphologically from the rate of development in the respirometers.

Oxygen measurements were made directly. The determination of CO_2 required the use of two respirometers, one containing KOH to determine the O_2 uptake, and another with distilled water only, to determine the net result of the exchange of oxygen and carbon dioxide.

By counting the ova in each manometer and reducing the change in height of the indicator fluid to a common denominator, the carbon dioxide (xCO_2) was determined by applying the formula, $xCO_2 = \left(h - \frac{xO_2}{kO_2}\right) kCO_2$ in which h is the observed change in the second manometer, xO_2 the calculated O_2 uptake from the first manometer, and kCO_2 and kO_2 the CO_2 and O_2 constants respectively, determined by calibration of the second manometer.

In the early experiments the manometers were read at hourly intervals, but since it was found that there was no significant variation from hour to hour, the results are here presented for twenty-four hour periods of time. In the later experiments, readings were made at hourly intervals for eighteen hours daily, but no readings were made between midnight and six o'clock in the morning. The number of ova used at one time in a respirometer varied from 350 to 1200.

EXPERIMENTS AND RESULTS

The oxygen used, the carbon dioxide given off, and the respiratory quotient were determined for ova with and without the albuminous coating at 30° C. Results of the gaseous exchange experiments are summarized in Table II, and graphically in Figure 2, which shows the O_2–CO_2 values in cubic millimeters per thousand eggs per day reduced to normal temperature and pressure. Each of the values given for oxygen consumed is the result of at least sixty, and each value for carbon dioxide the result of at least forty-five determinations, using 500 to 1100 eggs for each reading.

TABLE II.—*Gaseous exchange at 30° C. of ova A. suum (Gas figures expressed in cubic millimeters per 1000 ova)*

Days	With Albumin			Without Albumin		
	O_2	CO_2	R. Q.	O_2	CO_2	R. Q.
1	.30	.24	.80	2.44	2.23	.92
2	.30	.25	.83	2.44	2.29	.94
3	.33	.28	.85	2.49	2.39	.96
4	.39	.35	.90	2.30	2.12	.92
5	.39	.33	.85	2.49	2.32	.93
6	.46	.41	.89	2.24	2.12	.95
7	.48	.43	.90	2.08	1.92	.91
8	.40	.36	.90	2.12	1.87	.88
9	.51	.48	.94	2.12	1.82	.86
10	.51	.50	.98	2.14	1.89	.88
	4.07	3.63		22.86	20.97	

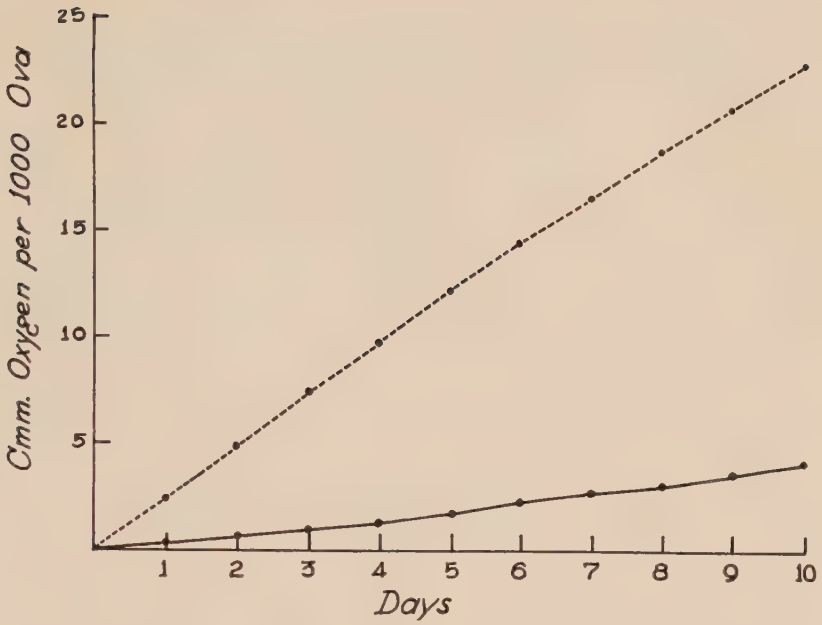


FIG. 2. Oxygen consumption of ova of *A. suum*. Ordinates, O_2 uptake in cmm. per thousand ova. Abscissae, time in days. Broken line, ova without albumin. Solid line, ova with albumin. Data from Table II.

The amount of oxygen used by untreated ova at 30° C. as determined by the method described above was 4.07 cmm. per thousand eggs for the period from the single cell stage to the production of a motile embryo. The rate of O_2 uptake was slightly but consistently higher in the later periods of development, and the respiratory quotient showed a regular progressive increase (save for the higher reading on the fourth day) from 0.81 on the first to 0.98 on the tenth day.

Eggs from which the albumin had been removed, used in ten days 22.86 cmm. of oxygen per thousand eggs—more than five times the amount of oxygen required by untreated eggs during a similar period of time. The respiratory quotient was less regular than that of untreated ova, beginning at .92 on the first day, rising to .96 on the third day with a drop to .86 on the ninth day, and a subsequent increase to .88 on the tenth day.

DISCUSSION

Since removal of the albuminous covering resulted in a five-fold increase in oxygen uptake during the ten day period, it would seem that some factor which was removed with the albumin restricted, directly or indirectly, the amount of O_2 taken into the egg. This additional oxygen must enter into various oxidative reactions in the cells for the respiratory quotient is about the same in treated as in untreated ova.

The slightly increased rate of oxygen uptake in the later days of development is at variance with Brown's (1928) finding that the O_2 used was constant from day to day for the duration of the period from the one cell stage to the formation of a complete embryo. Brown found the O_2 uptake from the one cell stage to embryonation to be 2.7 cmm. per 1000 ova. However, qualitative observations show that the amount of albumin present on individual eggs varies in different cultures and it may be that the relatively high oxygen consumption in the experiments reported here is due to the fact that the ova had less albumin than those used by Brown. Furthermore, since the complete removal of albumin resulted in a very marked increase in oxygen consumption, it may be that in the experiments to show the O_2 used by eggs with the albuminous coating there was sufficient dissolution of the albumin in the later periods to allow increasingly greater amounts of oxygen to enter the ova. This view is strengthened by the fact that there was no such increase in oxygen consumption in the later periods of development of those eggs from which the albumin had been removed.

SUMMARY

1. Removal of the albumin has no visible affect on development of ova at 30° C.

2. Removal of the albumin makes possible the development at 38° C. of 87% of the eggs through the tadpole stage, and about 11% of the eggs become embryonated.

3. An application of the Krogh respirometer indicates that respiration may be used in the interpretation of certain developmental factors.

4. The oxygen consumption is 4.07 cmm. per 1000 eggs for the period of development of untreated eggs at 30° C.

5. The oxygen uptake at 30° C. is increased more than five times by the removal of the albuminous coating.

6. The respiratory quotient increases from .80 at the beginning to .98 on the tenth day for untreated ova at 30° C. The R. Q. of the treated ova is less regular, varying from .86 to .96.

7. From the results described above, it would seem that the role of the albumin in development has been underestimated, for it modifies oxygen uptake significantly at optimum temperatures, and is at least partially responsible for failure of the eggs to develop at temperatures around 38° C.

Bibliography

Baillet, C. C. 1866.—Nouveau dictionnaire pratique de medicine, de chirurgie et d'hygiene veterinaries. Paris, 8. Article on helminths., 619–687.

Bodine, J. H. 1929.—Factors influencing the rate of respiratory metabolism of a developing egg (Orthoptera). Physiol. Zool., 2: 459–482.

Brown, H. W. 1928.—A quantitative study of the influence of oxygen and temperature on the embryonic development of the eggs of the pig ascarid (*Ascaris suum* Goeze). Jour. Parasit., 14: 141–160.

Cram, Eloise B. 1924.—The influence of low temperature and of disinfectants on the eggs of *Ascaris lumbricoides*. Jour. Agric. Res., U. S. Department of Agriculture, Washington, *27*: 167–175.

Crum, John D. 1932.—The influence of temperature and humidity on the development of the ova of *Ascaris lumbricoides* and *Trichuris trichiura*. Thesis, unpublished, State University of Iowa, Iowa City, Iowa.

Davaine, C. J. 1863.—Nouvelles recherches sur le developpement et la propagation de l'Ascaride lombricoide et du Trichocephale de l'Homme. Compt. Rend. Soc. Biol., Paris, 3: 261–265.

Dixon, M. 1934.—Manometric Methods. London, Cambridge University Press.

Fauré-Fremiet, M. E. 1913.—Le cycle germinatif chez *l'Ascaris megalocephala* Arch. anat. micr., 15: 437–736.

Inman, O. L. 1921.—Comparative studies on respiration XVII. Decreased respiration and recovery. Jour. Gen. Physiol., 3: 663.

Martin, H. M. 1926.—Studies on the *Ascaris lumbricoides*. Univ. of Nebr. Agric. Exp. Station Res. Bull. 37.

Nolf, L. O. 1932.—Experimental studies on certain factors influencing the development and viability of the ova of the human trichuris as compared with those of the human ascaris. Amer. Jour. Hyg., 16: 288–322.

Ogata, Seiji. 1925.—The destruction of ascaris eggs. Ann. Trop. Med. and Parasit., 19: 301–304.

Wharton, L. D. 1915.—The development of the eggs of *Ascaris lumbricoides*. Phi. Jour. Sci., B. 10: 19–25.

Zavadovskii, M. M. 1916.—Role de l'oxygen dans le presence de segmentation des oeufs de l'Ascaris megalocephala. Compte rend. Soc. de Biol., 68: 595–598.

ON THE POTENTIAL LONGEVITY OF VARIOUS HELMINTHS WITH A RECORD FOR A SPECIES OF *TRICHOSTRONGYLUS* IN MAN

By J. H. Sandground

Department of Tropical Medicine, Harvard Medical School

With few possible exceptions, parasitic worms do not pass more than one generation within their host, increase in the intensity of an infection being contingent upon the introduction of additional infective larvae from without. Consequently a knowledge of the natural, or normal, life-span of the parasite may determine the desirability of treating individual cases of infestation or may indicate the procedure that should be adopted in controlling the parasite on a larger scale. With a short-lived and not highly pathogenic helminth, it may be more politic to elaborate plans for the prevention of reinfection than to resort to medicinal treatment that may not always be efficacious and is sometimes accompanied by an element of danger to the host. On the other hand, when dealing with a long-lived parasite, widely distributed in a community or in a herd of animals, it is desirable to couple efforts to control the parasite in its extra-corporeal phase with treatment of the individual carriers. In several instances where agricultural live stock is involved, knowledge of the longevity of the parasite in its adult and free-living stages has led to the practice of seasonal administration of anthelmintics.

Important as information on this phase of helminth bionomics is recognized to be, dependable data is available for only a few of the long list of economically significant species. That such lacunae in our otherwise comprehensive knowledge of the biology of most of the common helminths should still persist is readily to be understood when it is realized how difficult of attainment are the conditions necessary to supply reliable information. The time when the infection became established must be known, at least approximately, and the infection must be followed continuously with the host adequately protected against reinfection or superinfection. Conditions which provide these requirements are difficult to secure where parasites of the lower animals are involved. But with certain parasites of man infections have sometimes been imposed experimentally to yield the desired information. Light has also been shed on this question by following cases of infection after the subject has left the region where the infection was contracted to reside in a region where reinfection cannot occur. Consequently more is known about the longevity of various species of human helminths than those of other animals.

Results secured from enquiries on this subject, are, however, not always free from complicating influences. We must draw a distinction between "longevity" and "potential or maximal longevity." The number of parasites that become established in a host at one time may determine the average longevity of the worm colony and in some cases a previous infection of the host may be a potent factor. It is of course well known that a parasite is likely to be short-lived in a host species to which it is not well adapted (the so-called abnormal host). While these aspects of the host-parasite relationship are very important in the natural balance of parasitic associations, the underlying forces are largely unknown and their consideration has necessarily been avoided in the following presentation of data collated from the literature.

TREMATODES

The little information that we have been able to collect concerning the longevity of flukes indicates that at least certain species of these worms persist for many years.

Clonorchis sinensis. In a Chinese who had migrated to Costa Rica, eggs of the liver fluke were found in the faeces some twenty-five years after the patient had left his native land (Moore, 1924). However, in dogs, according to Brumpt (1927), this species does not persist for much more than two and a half years.

Fasciola hepatica. The common liver-fluke of herbivores may live in experimentally infected rabbits for more than three years, according to the experiences of Montgomery (1931), while in cattle and sheep the parasites may persist for at least five years.

Schistosomum spp. It has frequently been noted that the various schistosomes of man live for many years. Kirkland (1928) records the case of an English soldier who contracted bilharziasis in South Africa during the Boer War (1900–1902) and in whose urine viable eggs of *S. haematobium* were being passed in 1927. Christopherson (1924) cites a case of 28 years' standing. Brumpt (*loc. cit.*) credits Maciel with the observation of eggs of *S. mansoni* continuing in the faeces of a Brazilian who, 19 years previously, had left the region where the disease is endemic. Although *S. japonicum* is also known to be long-lived, actual records are difficult to find. However, in the horse, experimentally established infection with this parasite have been noted to disappear in less than two years.

Paragonimus kellicotti is stated by Price (1929) [quoted by Taylor, 1933] to live for 6 years.

Gastrodiscus aegyptiacus, according to Vevers (*fide* Christopherson, 1924), has a record of 9 years in a zebra.

Metagonimus katsuradai Izumi, 1935, a small intestinal trematode of piscivorous mammals, including man, perhaps like other members of the Heterophyidae, is relatively short-lived. According to Izumi (1935), in experimentally infected mice, the longest period of parasitism was 32 days.

CESTODES

In their larval stages, such as the cysticercus and hydatid, tapeworms are known to persist for many years. However, according to the species, there is a great range of variation in the longevity of strobilated sexual individuals. Patients have presented the history of continuously passing segments of *Taenia saginata* for twenty to thirty-five years. Riley (1919) reported a case of *Diphyllobothrium latum* persisting for twenty-nine years under conditions that presumably barred the possibility of reinfection. In contrast to this extreme, Seddon (1932) reports that the common tapeworm of sheep (*Moniezia expansa*) does not live for more than 65 to 70 days.

Hymenolepis nana fraterna, the murine variety of the so-called dwarf tapeworm, was found by Shorb (1933) and by Hunninen (1935) to be even more ephemeral, persisting for only a few weeks. Whether the human variety, *H. nana nana* has a comparable short life span is not known and the ease of reinfection may render this question difficult to answer.

NEMATODES

Concerning the longevity of nematodes, more appears to have been recorded than for the other groups of helminths. Here, too, the life span differs widely according to the taxonomic status.

Trichinella spiralis is among the shortest lived of the parasites of man, it being commonly stated that the adults are soon sexually exhausted and are eliminated from the intestine within a period of a week or two. However, McCoy (1932) found that they persist in rats for two to three weeks and in guinea pigs for about 5 weeks.

Enterobius vermicularis. It has been stated that the life-cycle of the human pin worm is consummated within as short a time as two months. Hence it is inferred that a patient should spontaneously lose his infection if auto-infection from the ingestion of eggs is effectively prevented. However, it has been shown by Winfield (1933) that the common oxyurid of mice, *Heterakis spumosa,* may persist in the intestine for over 10 months.

Ascaris lumbricoides, the common round worm of man and pigs, is another relatively short-lived nematode. In certain rural sections of the United States, Cort and his associates have found that there is a rapid turnover of the infestations. To Otto (1932) this suggests that the

worms do not live for more than a year. The implication is drawn that for the control of ascariasis as a public health measure, improvement in general sanitation is likely to yield better results than medical treatment of the infected masses.

Oslerus osleri. The observation of Pillars (1935) that there was a cessation of the passage of eggs in a dog infected with this metastrongylid lung worm after about 5 months, is indicative of a short life span.

Dioctophyme renale, the giant kidney worm of dogs and other piscivorous mammals, is known to live for more than two years (Gray, 1933).

Contrasted with the aforementioned nematodes, the species of filarids affecting man are strikingly longevous. Microfilariae of *Loa loa* have been found circulating in the blood stream more than 15 years after the patient left Africa to reside continuously in Europe (Coutelen, 1935). Similarly, Knabe (1932) reports on the persistence of the microfilariae of *Wuchereria bancrofti* at least seventeen years after the patient could have contracted the infection. Fulleborn (1929) mentioned that he had kept dogs experimentally infected with *Dirofilaria immitis* in his laboratory at Hamburg for not less than seven years without loss of infection.

Although experimentally induced infections with *Strongyloides stercoralis* in man have been known to persist for as long as 24 years, the possibility of autoinfection precludes an unequivocal statement on the longevity of individual worms of this species.

Necator americanus and *Ancylostoma duodenale.*

Because of their public health significance, more attention has been paid to the question of the length of life of the hookworm of man than to any other helminth. In the literature are to be found estimates ranging from a few months to as long as twenty years. In experimentally induced infections, it has been reported by Miamazaki (1924), that hookworms (species not mentioned, but presumably *Necator americanus*) continue to produce eggs for as long as seven years. A colleague of the present writer furnishes the information that he harbors a light infection with this parasite that could not have been established less than twelve years ago.

Ancylostoma duodenale, which Looss believed capable of living for at least five years, has been shown by the recent experiments of Kendrick to persist for at least seven years. However, Chandler (1935) is of opinion that data secured from such single infection experiments are not indicative of what happens in nature where the host is exposed to continuous reinfection bringing into play the forces of host resistance which significantly alter the picture. Contrary to the views of Darling, Smiley

and others, who held that under natural conditions the hookworm load is slowly built up and equally slowly dissipated, Chandler's studies on prisoners in India by the egg count method lead him to the conclusion that in regions where there are well defined wet and dry seasons, the hookworm burden of the population is annually subject to rapid accretion which is paralleled by a comparable loss of worms after the rains end and the soil is sterilized of infective larvae. Doubtless, further observations will be forthcoming on this subject. It is doubtful whether the finding of Sarles (1933) that *Ancylostoma caninum* is eliminated spontaneously in a maximum period of from eleven months to two years after dogs had been experimentally infected, can be presented as indicating a comparable life span for the hookworms of man.

Trichostrongyles.

Concerning members of the family Trichostronglidae, other than such species as *Nippostrongylus muris* in rodents, which in the light of recent work appears to have a relatively brief life tenure, my review of the literature has uncovered no experiment-supported statement on potential longevity.

It was found by Stoll (1929) that under pastoral conditions of exposure to continuous reinfection, sheep may accumulate heavy infections with *Haemonchus contortus,* the twisted wire worm. As indicated by the gradual reduction and final cessation of the passage of eggs in the faeces in two lambs, Stoll found that these intense infestations were spontaneously lost within a period of less than five months. It is evident that the little known forces referred to under the term "host-resistance" have in these two animals led to the premature expulsion of the worms from their host. "Self-cure" of this type must be of fairly frequent occurrence under field conditions and to it may be ascribed the opinion (Monnig, 1930) that "the worms (*Haemonchus contortus*) do not live long" or, quoting a more definite statement from a popular pamphlet for farmers "sheep remain infected for a year or more." Can such statements be taken as an index of the maximum longevity of Haemonchus and related forms in sheep? Obviously it would be difficult in practice to secure accurate information on this subject from sheep exposed to the possibility of reinfection. This vitiating possibility has been eliminated in the conclusion that may be drawn from an experimental infection of man with a species of *Trichostrongylus,* details of which are now to be recorded.

In attempting to identify a strongyloid nematode parasitizing a missionary who had spent many years in Southern Rhodesia, Sandground (1929), by culturing the faeces, secured a small number of third stage larvae. On two occasions in January, 1928, a total of nearly 80 of these

infective larvae were swallowed. About two months later the characteristically shaped eggs were to be found in the faeces. The infection that had become established was evidently light for eggs were rarely to be found by examining faecal smears. By the standard Willis-Molloy concentration method, the number of eggs floated out of a 10 gram quantity of faeces was usually less than five. These eggs have always been fertilized showing that at least one male accompanied the one or more female worms which became established. Faecal examinations two or three times a year have shown no tangible diminution in the numbers of eggs passed and the infection is still persistent nearly eight and a half years after its establishment.

Unfortunately we have not been able to determine the specific identity of the parasite involved. With the object of expelling the worms on two occasions 5 cc. tetrachlorethylene and on a third occasion 4 cc. of carbon tetrachloride have been taken but these treatments have been ineffective. With the few infective larvae that have been accumulated after culturing considerable quantities of faeces, fruitless attempts have been made to establish the adult worms in a rabbit and a dog. However, despite our failure to procure specimens of the adults for identification, the character of the eggs and the morphology of the larvae indicates with a high degree of probability that the parasite involved is a species of *Trichostrongylus*. It is possibly *T. colubriformis* (Giles), a species very common in the sheep of South Africa and one that is recorded as a not infrequent parasite of man in various parts of Africa.

Bibliography

Christopherson, J. B. 1924.—Longevity of Parasitic worms: the term of living existence of Schistosoma haematobium in the human body. Lancet, April 12th, p. 742.

Coutelen, F. 1935.—La longévité de la filaire *Loa loa* (Guyet, 1778) et des embryons de filaires. A propos d'un cas de filariose diurne. Bull. Soc. Path. exot., *28*: 126.

Gray, H. 1933.—*Dioctophyme renale* in the kidneys of a dog. Vet. Record, 13: 276.

Izumi, M. 1935.—Studies concerning a new species of Metagonimus and its life-cycle. Kitasato Arch. Exper. Med., 12: 362.

Kirkland, H. T. 1928.—A case of Schistosomiasis presenting some unusual features. Jl. Trop. Med. & Hyg., 31: 78.

Knabe, K. 1932.—Beitrag zur Dauer von Filarieninfektion. Arch. f. Sch. u. Tropenhyg., 36: 496.

McCoy, O. R. 1932.—Size of infection as an influence on the persistence of adult Trichinae in rats. Science, 75: 364.

Minamizaki, Y. 1934.—A study of the viability of hookworms in the intestine. Far Eastern Assn. Trop. Med., 9th Congress, p. 587.

Montgomery, R. F. 1931.—On the longevity of *Fasciola hepatica* in experimentally infected rabbits. Jl. Helminthology, 9: 209.

Moore, D. 1924.—Note on the longevity of *Clonorchis sinensis*. U. S. Pub. Health Repts., 39: 1802.

Otto, G. F. 1932.—Ascaris and Trichuris in the Southern United States. Jl. Parasit., 18: 200.

Pillers, A. W. K. 1935.—Some remarks on the clinical aspects of chronic tracheobronchitis of dogs due to *Islerus osleri* (Cob., 1879). Vet. Record, 15: 62.

Riley, W. A. 1919.—The longevity of the fish tapeworm of man, *Diphyllobothrium latum*. Jl. Parasit., 5: 193.

Sarles, M. P. 1929.—Length of life and rate of loss of dog hookworm, *Ancylostoma caninum*. Amer. Jl. Hyg., 10: 667.

Seddon, H. R. 1931.—The development in sheep of immunity to *Moniezia expansa*. Ann. Trop. Med. & Parasit., 25: 431.

Taylor, E. L. 1933.—The longevity of parasitic worms with special reference to a report of the occurrence of *Dioctophyme renale* in this country. Vet. Record, 13: 407.

COMPARATIVE STUDIES ON CERTAIN SPECIES OF *DIPHYLLOBOTHRIUM*

JUSTUS F. MUELLER,

New York State College of Forestry, Syracuse, N. Y.

In a previous paper (Mueller, 1935), the writer described as new a species of *Diphyllobothrium* from cats in the Syracuse area, under the name *D. mansonoides*. At that time, and since, doubt has been entertained in some quarters as to the validity of this species. Skinker (1935) states: "In the description of *Diphyllobothrium mansonoides* Mueller, 1935, no morphological details are given which the present writer accepts as constituting adequate characters for specific differentiation of this species from *D. mansoni* (Cobbold, 1882) Faust and Wassell, 1921. *D. mansonoides* is, therefore, considered a synonym of *D. mansoni*." At the time of the original description, comparisons with *D. mansoni* were made on the basis of the published descriptions of that form. Since then, however, material of this species has been secured for comparative morphological study, the results of which are herewith presented.

The material used consisted of 19 specimens of *D. mansonoides* collected from Syracuse cats since 1933. No further data have been secured on the possible occurrence of this worm in dogs. To date, 212 cats have been examined, of which 10 were found infected with the worm, making an incidence of 4.6 per cent. These cats were examined during the months from February to June, inclusive, of different years, and of the 10 infested cats, 5 were found during the month of March. Unfortunately, our examinations were not sufficiently distributed to indicate whether there is a seasonal variation in incidence or not. Six of the 10 cats harbored a single worm; one had 2 worms, another 3, and the remaining two cats 4 each. I am greatly indebted to two of my former students, Mr. Carlton Herman and Mr. Robert Perry, who examined many cats for me, and who assisted in other ways in the study of this parasite.

Material of all of the *mansonoides* taken to date has been studied in detail to determine the limits of variation. Whole mounts were made of pieces from each strobila. Nineteen sets of serial sections were prepared. The general measurements of the species, as given previously, must be emended. The maximum length, formerly given as 60 cm., must be raised to 140 cm. (55 inches); the maximum width from 7 mm. to 10 mm. On April 16, 1936, a large pregnant female cat was found to harbor three unusually large worms, the biggest of which had the dimensions indicated. The other two worms were respectively 89 cm. (35 inches)

long, by 8 mm. in greatest width; and 102 cm. (40 inches) long, by 9 mm. in greatest width. However, many mature specimens are of much smaller size, from 10 to 14 inches in length.

In the original description of *mansonoides,* the fully developed coracidium within the egg was said to possess only one flame cell. However, as a result of further study on new material, it can now be stated that two flame cells are present. In this respect the coracidia of *D. mansonoides* and *D. latum* are alike. It is seldom that an egg can be found in which both flame cells are equally active. Usually only one is active, and the other quiescent, and for this reason, ordinarily only a single flame cell can be identified with certainty.

Dikmans (1931) recorded a tapeworm taken from a cat at Jeanerette, La., as *D. mansoni.* This specimen was secured from the U. S. Bureau of Animal Industry for study. The material is not typical of *mansoni,* but is identical in all respects with *D. mansonoides* from Syracuse. In its present condition it consists of a series of fragments, the longest piece 15 inches (38 cm.) long, and the greatest width 8 mm. Judging from the character of these fragments the complete worm must have been at least 30 inches (76 cm.) long. The scolex is of the same form and size as that of other *mansonoides,* the neck 7 mm. long. Representative pieces of the strobila were sectioned in the frontal, sagittal, and transverse planes, and whole mounts were prepared.

A specimen of *D. mansoni,* from Japan, was given the author by Dr. Teunis Vergeer, of Hope College, Mich. According to information received, this material was "from a domestic cat, collected on September 19, 1926, by Dr. S. Yamaguchi." It is a small worm, about 31 cm. in length, with maximum width of about 3 mm. The scolex is not markedly different from that of *mansonoides,* but the edges of the bothria are thinner and more developed. The neck is 4 mm. long.

The writer also examined a specimen of *D. mansoni* forwarded to him by Dr. G. F. Otto, of Johns Hopkins University. This worm had been collected from a cat in Panama by Dr. A. C. Foster, of the Gorgas Memorial Laboratory, and provisionally identified as *D. mansoni.* This diagnosis is confirmed. The scolex is lacking. It consists of a strobila about 38 cm. long, by 7 mm. maximum width. The anterior end lies very near the neck region. Judging from the appearance of the posterior proglottids, which are similar in proportion and state of activity to those found near the middle of most worms, the worm must reach a considerably greater length than this specimen would indicate, probably as much as 60 to 70 cm. Both of these worms were studied in the form of stained whole mounts, and also sectioned in all three planes.

For further comparison, certain material of *D. latum* was also studied, namely, fragments of an adult worm raised experimentally in a

bear by Dr. Teunis Vergeer, and given by him to the writer; also a complete specimen passed after treatment by a female patient in Syracuse (case reported elsewhere). This material was sectioned, and also prepared as whole mounts.

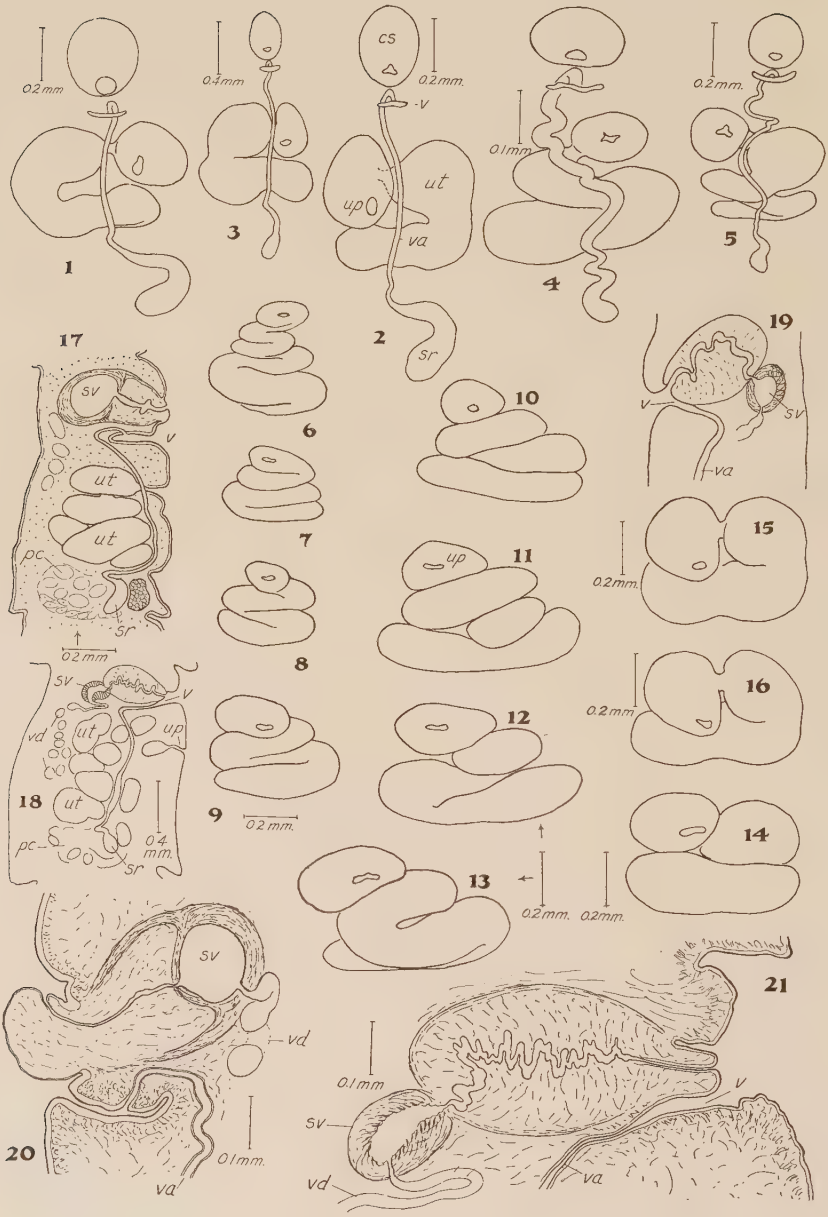
Comparison of *D. mansonoides* and *D. mansoni*

The uterus of *D. mansonoides,* as previously described, consists of two series of coils, an anterior (outer) series, and posterior (inner) series, joined by a connecting duct. The posterior coils have thin delicate walls. The connecting duct passes to the dorsal surface of the anterior uterine mass, and performs several small, irregular loops, also having delicate walls, and not visible from the ventral surface. Finally the uterine tube passes into a large terminal loop with deeply staining, thick, glandular walls. This region is normally all that is seen of the anterior part of the uterus when viewing whole mounts, and has the form of a U placed on its side. The anterior limb is constricted near the middle, dividing off a terminal chamber or ovejector. This U-shaped terminal loop of the uterus is so proportioned as to be rather rectangular and symmetrical, and remains inflated, and of constant form, whether or not it is filled with eggs. Extra loops in this heavy walled portion do not occur. In all of my specimens the outer uterine coils are remarkably constant, and form the best character for diagnosing the worm.

In contrast to this condition, the uterus of *D. mansoni,* although like that of *mansonoides* in general plan, has a varying number of loops in the terminal heavy walled portion. There are usually four transverse limbs, as compared with the two of *mansonoides,* but the number varies in different proglottids. Rarely a proglottid has a uterus almost as simple as that of *mansonoides* (fig. 14), but against this, other proglottids of the same chain may have as many as seven loops of irregular disposition and length. In no two proglottids of the same strobila is the uterus of *mansoni* exactly alike, whereas, in *mansonoides,* in different proglottids of a single chain, or in different chains, the uterus is always of the same, simple form. This variability in the outer uterine coils is characteristic of *D. mansoni,* while uniformity in the outer coils is equally characteristic of *mansonoides.*

The vagina of *mansonoides* makes a deep loop between the anterior and posterior uterine coils, and opens abruptly upon the anterior wall of a wide terminal vestibule, or vulva. Sections show that *D. mansoni* possesses the same two features, and the drawings of Faust, Campbell, and Kellogg indicate that the same type of vulva occurs in other members of the subgenus Spirometra.

D. mansoni and *mansonoides* are unlike, however, in that the vagina of the latter passes posteriad from its vestibule in an approximately


0.2mm
1
0.4mm
3
cs
0.2mm.
v
up
ut
va
sr
2
0.1mm
4
0.2mm.
5
17
sv
v
ut
ut
pc
sr
0.2mm
6
7
8
9
0.2mm.
10
up
11
12
13
0.2mm.
0.2mm.
19
v
sv
va
0.2mm.
15
0.2mm
16
14
sv
v
vd
ut
up
18
ut
pc
0.4 mm.
sr
sv
vd
20
0.1mm.
va
21
0.1mm
v
sv
vd
va

straight path in the median line (figs. 1–3), whereas the vagina of *mansoni,* in traversing the same distance, is thrown into lateral undulations of considerable amplitude (figs. 4, 5). It has been determined with certainty that this difference is real and not due to states of contraction.

Comparison of the subgenera *Spirometra* and *Diphyllobothrium*

Faust, Campbell, and Kellogg divided the genus *Diphyllobothrium* into the above subgenera on the basis of the difference in the uterus (coiled spirally in Spirometra; rosetted in *Diphyllobothrium*), and the eggs (with pointed ends in Spirometra; rounded ends in *Diphyllobothrium*). Further differences between certain species of these subgenera are here pointed out in the belief that these differences will be found to be of subgeneric value.

In *D. latum,* from both human and bear hosts, the cirrus opens into a funnel shaped sinus, which, without any line of demarcation, tapers into, and is continuous with, the vagina. In Spirometra (*mansoni* and *mansonoides*), on the other hand, the cirrus opens to the exterior separately, a short distance anterior to the female genital pore, and the vagina is very sharply set off from its terminal vestibule. Thus *D. latum* (figs. 18, 19,

---

EXPLANATION OF FIGURES

Figs. 1–5 and 17–21 represent graphic reconstruction from serial sections.

abbreviations

cs—cirrus sac
pc—posterior coils of uterus
sr—seminal receptacle
sv—seminal vesicle
up—uterine pore
ut—anterior coils of uterus
v —vestibule or vulva
va—vagina
vd—vas deferens

FIGS. 1, 2. Ventral view of cirrus sac, anterior coil of uterus, and vagina in two specimens of *D. mansonoides* from Syracuse.

FIG. 3. Vagina and uterus of *D. mansonoides* collected by Dikmans in Louisiana.

FIG. 4. Vagina, anterior coils of uterus, etc., in *D. mansoni* from Japan.

FIG. 5. The same in a specimen of *D. mansoni* from Panama.

FIGS. 6–9. Anterior coils of uterus in different proglottids of same specimen of *D. mansoni* from Japan.

FIGS. 10–14. Anterior coils of the uterus in different proglottids of the same specimen of *D. mansoni* from Panama.

FIG. 15. Anterior coils of uterus in *D. mansonoides* from Syracuse. This pattern is constant in all proglottids and all worms.

FIG. 16. Anterior coils of uterus in *D. mansonoides* from Louisiana, Dikmans' specimen. All proglottids in the strobila have this type of uterus.

FIG. 17. Composite drawing of sagittal section of *D. mansoni* from Panama, showing character of cirrus sac, vagina, uterine pore, etc.

FIG. 18. Composite sagittal section of *D. latum* from bear. Compare cirrus sac, and vagina with fig. 17.

FIG. 19. Cirrus sac and opening of vagina in *D. latum* from human.

FIG. 20. Detail of cirrus sac, vulva, and vagina in *D. mansonoides* from Syracuse cat.

FIG. 21. Detail of cirrus sac, vulva, and vagina in *D. latum* from bear. The muscular seminal vesicle is outside of the cirrus sac. Compare fig. 20.

21) possesses a single, common, genital pore, while *D. mansoni* and *D. mansonoides* have separate male and female pores.

The cirrus sac in *D. latum* is traversed by a tubular canal, much folded, but lacking expansions along its course, and the terminal portion of the vas deferens, contiguous with the cirrus sac, consists of a large muscular bulb, or seminal vesicle (figs. 18, 19, 21). However, in *mansoni* and *mansonoides* this muscular chamber is incorporated in the cirrus sac (figs. 17, 20).

In *D. latum,* several folds of the uterus lie between the vagina and the ventral surface of the proglottid (fig. 18). In *mansoni* (fig. 17), or in *mansonoides,* however, the uterus is entirely dorsal to the vagina. It also appears that the dorsal loop of the vagina, between the inner and outer coils of the uterus, is more pronounced in the *mansoni* group than in the *latum* group.

In addition to the difference in shape of the ova, which has already been mentioned, it is probable that there are also consistent differences in the coracidia of these subgenera. The coracidium of *D. latum* is relatively sluggish, and lacks polarity, swimming with a slow, rolling motion, the hooks of the oncosphere being successively turned in all different directions with reference to the path of motion. In *mansonoides,* however, the coracidium swims with great speed, and has definite polarity, always carrying the hooks at the posterior pole, while the cilia beat backward from a point on the surface directly opposite.

DISCUSSION

A possible objection to this study lies in the fact that the writer had only limited material of *D. mansoni* for comparison with *D. mansonoides.* However, this criticism is answered by the generous quantity of *D. mansonoides* which was studied. Were the two forms really identical, it is reasonable to believe that in this number of specimens of *D. mansonoides* some would have been found showing the typical morphology of *mansoni.* Such were not found. Considerably more variation occurred in a single specimen of *D. mansoni* than could be found in all of the *mansonoides* studied.

When the author originally described and named *D. mansonoides,* he did so with reservations: "It is possible that later comparative study may force this species into synonymy with some other form. . . ." It is now held, as a result of the above study, that *D. mansonoides* is unquestionably a valid species, and readily distinguished from its close relative *D. mansoni* on the character of the outer uterine coils and the vagina. The two species are, however, closely related, and hence there is probably a close parallel in life history.

Human cases of sparganosis have been reported for this country (Texas and Florida). Speaking of *D. mansoni,* Faust, Campbell, and Kellogg remark (page 579) "Proof of the presence of this species in Australia or Texas, where '*Sparganum mansoni*' infections have been reported must await experimental confirmation." With the emended identification of Dikmans' material from Louisiana, it now appears that *D. mansoni* has not to date been found in the United States, but is apparently replaced in this territory by *D. mansonoides.* In view of this fact it is possible that the reported cases of Sparganum infection for this country represent cases of infection with the larval stage of *D. mansonoides.*

The plerocercoid of *mansoni* in the Orient is known to occur in frogs, snakes, and possibly also in small mammals and birds. A survey will be undertaken during the summer of 1936 to determine whether these hosts carry plerocercoids in this region. No records of spargana in these small animals are so far known for this continent.

The writer is of the opinion that when the members of the genus *Diphyllobothrium* are more completely known, the members of its subgenera will be separated not only be differences of egg, uterus, and host selection in the plerocercoid stage, but also by characters of the cirrus and vagina, and by the behavior of the coracidium. Should it be demonstated that this is actually so, it may be necessary to raise these subdivisions to full generic rank.

SUMMARY

1. Specimens of *Diphyllobothrium mansoni* from Japan and Panama have been compared in detail and found to be the same species.

2. Dikmans' specimen of *"D. mansoni"* from a cat in Louisiana (1931) has been studied and determined to be *D. mansonoides* Mueller.

3. *D. mansoni* and *D. mansonoides* have been compared in detail and found to be separate species on the basis of characters of the uterus and vagina.

4. Further differences are found between *D. latum* on the one hand, and *D. mansoni* and *mansonoides* on the other, which are probably of general value in separating the two subgenera *Spirometra* and *Diphyllobothrium.* These characters have to do with the structure of the cirrus, the vagina, and the polarity and behavior of the coracidium.

5. From a total of 10 infected cats, 19 specimens of *D. mansonoides* have been collected to date. In all, 212 cats have been examined. The incidence of the worm in cats in this region appears to be about 4.6%. No further information has been obtained relating to the possible occurrence of this worm in the dog.

References Cited

Cram, E. B. 1927.—*Diphyllobothrium mansoni* in Porto Rican cat. Jour. Parasit., 14: 70.

Dikmans, G. 1931.—An interesting tapeworm from a cat in Louisiana. Jour. Parasit., 18: 47.

Faust, Campbell, and Kellogg. 1929.—Morphological and Biological Studies on the Species of Diphyllobothrium in China. Amer. Jour. Hyg., 9: 560–583.

Moore, J. T. 1915.—*Sparganum mansoni.* First Reported American Case. Amer. Jour. Trop. Diseases, 2: 518–525.

Mueller, J. F. 1935.—A Diphyllobothrium from Cats and Dogs in the Syracuse Region. Jour. Parasit., 21: 114–121.

Skinker, M. S. 1935.—Miscellaneous Notes on Cestodes. Proc. Helm. Soc. Wash., 2: 68.

A QUANTITATIVE STUDY OF THE NEMATODES FROM A SELECTED GROUP OF EQUINES IN PANAMA[1]

A. O. Foster

Helminthologist to the Gorgas Memorial Laboratory, Panama, R. P.

INTRODUCTION

During June, July and August, 1935, an opportunity was provided to examine at autopsy for the recovery of parasitic worms, a total of 48 horses and mules owned by the Panama Canal Department of the U. S. Army. As the infestation of each animal was studied quantitatively, in so far as possible, as well as qualitatively, it has been felt that the findings upon this group of equines, as outlined in the following pages, contribute to our knowledge of the occurrence and relative abundance of helminthic species in equines, particularly those of this locality. In addition, these data augment materially the limited information which is at present available upon the localization of Strongylid species within the large bowel and upon the adaptation of the several species to different kinds of equines (horses or mules). At the same time, it has seemed that these data present a reasonably accurate picture, both quantitatively and qualitatively, of the verminous infestations of Army equines in the Panama Canal Zone.

Selectiveness of Animals and Miscellaneous Information

From the helminthological viewpoint, it must be emphasized that the present series of equines is a highly selected group. In the first place, all were imported into the Canal Zone, and, although the periods of residence in the Zone were not less than 5 years in any case, it cannot be concluded, on the basis of these data alone, that the species encountered in these animals are indigenous to equines of Panama. In the second place, the equines of this series presented, in contrast to other animals which we have studied, a condition of extremely light worm-infestation. Much of this may perhaps be attributed to their excellent general condition and to the fact that, for the most part, they were stabled rather than pastured. Another factor of some significance is the care which is given to Army animals, a consideration of which suggests that the worm burdens of these animals probably represent about the minimum practical level which can be attained by the intelligent application of such

[1] The author wishes to acknowledge his indebtedness to Lt. Col. C. W. Greenlee, V.C., U. S. A., whose constant cooperation and interest made this survey possible. It is a pleasure to acknowledge also the able technical assistance of Sr. Pedro Ortiz Orsini.

measures of prevention and treatment as are now known. It was, of course, these low-grade infestations which permitted, under the conditions of these autopsies, a reasonably accurate quantitative study of the various species.

In this series were 17 horses and 31 mules, ranging in age from 9 to more than 24 years, and having resided in the Canal Zone for from 5 to 19 years at the time of autopsy. They were sacrificed because of a condition of incipient lameness, the cause of which, although not thoroughly understood and perhaps of a nutritional nature, may be definitely regarded, at least, as non-verminous. It may be said, then, that the animals of this series, except for the early articular lesions responsible for their lameness (a condition which was being studied by the Veterinary Corps of the Army, under Lt. Col. C. W. Greenlee) enjoyed the same generally good physical condition which one observes regularly in Army animals.

Methods of autopsy and worm-collection.

In the handling and identification of parasites a number of routine technics were used which need not be reviewed here, although a brief statement upon the conduct of the autopsies and worm-collections has seemed advisable. The animals were killed by gun-shot and opened immediately. The Great Colon was drawn out and the dorsal and ventral portions separated by ligature of the pelvic flexure. The cecum was not ligated from the ventral colon as it had been noted in earlier autopsies that nothing was gained by so doing, a technic which has been further justified by the data upon the differential distribution of species obtained during these studies. At this point, the body cavity was completely emptied of its organs, including the aorta. Although portions of the Ligamenta Nuchae, Bursati, and of the so-called Dhobie Itch lesions were occasionally taken to the laboratory for examination, it is to be admitted that no systematic search was made for certain of the filarial worms which have been encountered now and then in intimate association with ligaments and tissues of the neck and legs. With this exception, the search for verminous lesions and parasites was rather complete. The colon and cecum was rapidly freed of attachments, which could be done easily without rupture in most cases, and then divided into three portions, viz.: the cecum, ventral colon, and dorsal colon. These portions were laid out on a smooth concrete floor, apart from each other, and opened by cutting lengthwise along the surface to which the mesocolon had been attached. The content of each portion was rolled out upon the floor and the intestine was placed for examination, lining uppermost, upon a very convenient table of large wooden boxes. A laboratory helper, who understood considerable about the

various species of equine helminths, was assigned to the examination of each portion. Usually the intestine was being examined in from fifteen minutes to a half-hour after the animal was shot. First the mucosa was rapidly examined for the attachment of worms, and notes were recorded upon this and any other interesting phenomena which were observed. Then the worms were collected from the surface of the contents, afterwards from the intestinal mucosa. At intervals during the collection, the contents were again examined, since, by observation, it was learned that the Strongylid species tend to come to the surface of the intestinal contents. After all of the visible parasites had been collected by this method, the contents were examined in small portions. Afterwards, the contents usually were pressed out on the floor, using either the hand or the sole of one's boot, and allowed to remain on the wet surface for a short interval during which the portion of the intestine was examined further. In this way worms were frequently recovered from the surface of the flattened-out contents. Then the contents were carefully pushed to one side, and any worms which were on the wet floor were collected. After further cursory examinations both of the contents and of the intestinal wall, which in many instances failed to yield any more worms, the collections were regarded as satisfactory.

This procedure has been outlined in some detail, because it has seemed to be the most practicable method for a quantitative approach to the study of equine parasites. This technic takes advantage of the readily observable fact that the Cylicostomes live in intimate association with the mucosa[2] and on the surface of the content-mass, and obviates the necessity of screening, a method of worm-collecting which gives very unsatisfactory results when applied to the intestinal contents of equines. This latter method is impracticable because of the large size of the particles of debris compared to the relatively small size of many of the Cylicostomes.

The stomach and small intestine were also examined for parasites and verminous lesions.

Summarily, it may be stated that worm-collections routinely were made into five separate bottles used for the following regions; cecum, ventral colon, dorsal colon, stomach and mesenteric arteries, and body cavity, etc. These bottles, and inked labels for putting in them, were prepared in advance. Other smaller bottles, for special uses, such for example as determining specifically a helminth of conspicuous color or one found attached, were carried regularly in the autopsy kit. The

[2] In making this statement, it is not desired to enter into the discussion of the extent to which the Cylicostomes are *normally attached* to the lining of the colon and cecum.

worms were collected into normal salt solution and later, in the laboratory, were fixed, cleared, identified, and counted. Among other equipment, there was also included a note-book in which rather complete notes were kept upon each autopsy.

Thoroughness of worm-collections

From the above discussion, it is not to be supposed that our technic is regarded as having been completely adequate for the recovery of all of the parasites. In each instance, a notation was made after finishing an autopsy, upon the degree of completeness of the helminthic collections. Our records show that there were 18 autopsies at which it was felt that "practically all" of the worms were taken, 9 cases where it was known that only a portion of the total number of smaller Cylicostomes were taken, and 21 cases, for which it was recorded that practically all of the worms were taken, *except* some of the smaller Cylicostome species from either the ventral colon or the dorsal colon. In these cases it is considered that the specimens missed from the dorsal colon were mainly of the species *Cylicostephanus longibursatus,* and from the ventral colon *Cylicocyclus nassatus.* Since these are among the most abundant species of *Strongylidae,* it has been felt that the relative proportions of Strongylid species as calculated from our data, are approximately correct. Moreover, for the larger species of *Strongylidae* it is felt that the collections were as nearly complete as possible. In spite of this, the smaller species were the most abundant, a consideration which encourages our feeling that these studies, in general, are fairly reliable from the quantitative, as well as from the qualitative, viewpoints.

Qualitative nature of the infestations

It may be permissible to point out at this time that no Trematodes were encountered in these autopsies, and that, of the Cestodes (genus *Anoplocephala*) which were so abundantly represented in the native equines which we have studied, only a single specimen (*A. perfoliata*) was present in this whole series of 48 animals. It might also be remarked that no "bots" (*Gastrophilus* larvae) were present in these animals. The nematodes, however, were found to represent 5 families, 17 genera, and 39 species.[3]

OBSERVATIONS AND DATA

Order *Myosyringata* Ward, 1917

Suborder *Strongylata* Railliet and Henry, 1913

[3] In the following pages, we have followed, in general, the nomenclature which is at present in use by the Zoological Division, Bureau of Animal Industry, U. S. Department of Agriculture.

Superfamily *Strongyloidea* Weinland, 1858; Hall, 1913
Family *Strongylidae* Baird, 1853

Within this family are included nearly all of the Nematode species which infest the large bowel of equines. From the present series of animals there were taken 32 different species belonging to 12 genera and 2 subfamilies within this family.

Although desirable, it has been found impracticable to present in tabular form the data upon the localization and quantitative occurrence of each of the species in the individual animals. It is felt, however, that the more interesting analyses and interpretations are presented in the zoologically-arranged discussions which follow.

Subfamily *Strongylinae* Railliet, 1893

This subfamily was represented by 3 genera and 8 species. It includes most of the larger Strongylid species, and particularly those which can be readily observed, for the most part, to be firmly attached to the wall of the cecum or colon. Morphologically, the species of this subfamily are distinct from the other equine species mainly by their conspicuously large, subglobular buccal capsules. In this report, about one-seventh of the total Strongylid fauna has been assigned to this subfamily and it includes some of the commonest and most frequently occurring species.

Genus *Strongylus* Mueller, 1780

The three species of this genus known to parasitize horses and mules were among the commonest of parasites from this series of animals. For what they lacked in abundance, compared to some of the smaller Strongylid species, they were compensated by their high incidence and conspicuousness. All three species were encountered together in 36 (75 per cent) of these equines; while of the other animals, 10 harbored two species, one of which was, in each case, *S. vulgaris,* and, in two instances the latter species occurred as the sole representative of the genus. Horses and mules alike appeared to be good natural hosts for all three species. It may be permissible to remark that these worms are not red or blood-colored as is often stated; rather they are distinctly dark blue, except the very young specimens, with frequently a more sanguineous aspect over the anterior fifth of the worm.

Strongylus equinus Mueller, 1780

This species occurred in 41 animals (85 per cent), of which 26 (84 per cent) were mules and 15 (88 per cent) were horses. Infestations were light, averaging 8 to 9 worms per animal, while the largest

single infestation was only 39 worms, of which number 37 were taken from the cecum. That this region is the slightly preferred habitat of *S. equinus* is further evidenced by the fact that 72 per cent of the specimens were taken from the cecum, 27 per cent from the ventral colon, and less than 1 per cent from the dorsal colon. It is felt that our data are sufficiently accurate to say also that this was the 15th commonest Strongylid species, being the 5th commonest of the cecum, the 14th of the ventral colon, and the 21st of the dorsal colon. Although only slightly less abundant than the species which follows it may be said to have been the least common species of the genus. In length, female specimens averaged about 41.5 mm. and males about 28.7 mm.

S. edentatus (Looss, 1900)

The incidence of this species paralleled closely that of *S. equinus*. It also was found in 41 animals, of which 25 were mules and 16 horses. Infestations averaged 10 to 11 worms, the largest number from one animal being 59, all of which, in this case, were taken from the ventral colon. As in the case of *S. equinus,* this species was encountered throughout the large bowel, although it differs from both the other species of the genus in its preferred localization, as evidenced by the fact that 84 per cent of the specimens were taken from the ventral colon. Only 15 per cent occurred in the cecum and less than 1 per cent in the dorsal colon. It was, however, the 6th most abundant species of the cecum, the 9th of the ventral colon, and the 17th of the dorsal colon. Its rank among the Strongylid species was next above that of *S. equinus*. Female specimens averaged about 36.5 mm. long, and males about 24.7 mm.

S. vulgaris (Looss, 1900)

This species was by far the commonest of the genus and was the only helminth encountered at every autopsy. It accounted for about 82 per cent of the total number of specimens belonging to the genus *Strongylus*. The infestations varied from 1 to 287 worms per animal, averaging about 87. It was the characteristic Strongylid species of the cecum,where about 96 per cent of the specimens occurred. It was infrequently met with in either the ventral colon (3 per cent) or the dorsal colon (1 per cent). Of the 32 Strongylid species, *S. vulgaris* was the 4th most abundant. This species, the smallest of the palisade worms, averaged 22.8 mm. in length for the females, and 16.7 mm. for the males.

Larvae of *S. vulgaris,* in various transitional stages, were recovered from either the right or the anterior branch of the Great Mesenteric Artery in 36 cases (75 per cent). Twenty animals harbored over 5

larvae each in those vessels, while 16 harbored less than this number. Compared to our observations of verminous aneurysm in native equines, it might be remarked that this is a particularly favorable finding.

Genus *Triodontophorus* Looss, 1901

The individual species of this genus were encountered in both horses and mules, although it appears from our data that the horse is the slightly preferred host and the ventral colon the usual habitat. All 4 species were found together in the same host upon two occasions, 3 (and only 3) species occurred together in one host 11 times, 2 species occurred 12 times, and one species only (usually *T. minor*) was found in 16 animals. Although seven animals harbored no parasites of this genus, it is interesting that two or more species were present at over half of the autopsies, and that three species were found together in about one-fourth of them. It is interesting also that, from the 41 animals harboring *Triodontophorus* spp., there were recovered and identified an even 800 specimens representing this genus, whose distribution as to species was as follows: *T. minor* 668 (83.5 per cent) *T. serratus* 74 (9.2 per cent), *T. tenuicollis* 82 (5.3 per cent), *T. brevicauda* 16 (2 per cent).

Triodontophorus serratus (Looss, 1900)

This species was recovered from 22 animals (46 per cent), more than half of which were horses. Since there were many more mules than horses covered in this survey, it follows that a much higher percentage (88 per cent) of the horses harbored this species than of the mules (22 per cent). The largest number of worms taken from one animal was 11, all of which in this instance were found in the cecum. This is the only species of the genus which occurred in the cecum, and likewise the only one which did not occur in the dorsal colon. Of the limited number of specimens recovered, 63 per cent were from the ventral colon and 37 per cent from the cecum. Although these figures indicate a slight preference for the ventral colon, it might be remarked that, not infrequently, in individual cases, like that above, *T. serratus* was restricted to the cecum. There were 5 such cases, while, on the other hand 11 animals harbored this species in the ventral colon only, and 6 yielded this parasite from both regions. This was one of the rarer species, ranking 17th among the Strongylid species from these animals, although it was the 8th commonest from the cecum and the 16th from the ventral colon.

It was with some hesitancy that the parasites discussed above were assigned to the species *T. serratus*. Our specimens satisfy in every particular the description given by Boulenger (1916) for *T. intermedius*

Sweet, 1909. G. Theiler (1923), in synonymizing this with Looss' type species, has admittedly shown that these two species are more closely allied then either Sweet or Boulenger had allowed, yet there still remain the consistently smaller size and conspicuously circular mouth-collar of the "*intermedius*"-type which appear to cast a reasonable doubt upon the identity of this and Looss' species. *T. serratus* was described as having a well-developed mouth-collar "flat, rather than high," and the original figures agree with this description. More than anything else, it has seemed unlikely that Looss was viewing the same species that we have observed when he figured *T. serratus*. In the event that both species, after more thorough study, shall be accepted as valid, it will follow that the species here reported is *T. intermedius* Sweet, 1909; *partim* Boulenger, 1916.

T. minor (Looss, 1900)

This was the commonest species of the genus. It was recovered from all of the horses and from 22 (71 per cent) of the mules. The largest number recovered from one animal was 73, of which 71 were taken from the ventral colon and 2 from the dorsal colon. Looss commented that *T. minor* was remarkable for its habitat in the posterior colon, although G. Theiler (1923) observed that this species, in South Africa, was common in the ventral as well as in the dorsal colon. Of the 668 specimens taken by us, 596 (89 per cent) came from the ventral colon, while only 72 (11 per cent) were recovered from the dorsal colon. It is our opinion that this, in common with the other species of the genus, is essentially a ventral colon form. *T. minor* has been considered one of the commoner species, being the 12th commonest of the family, and ranking 7th in both the ventral and dorsal portions of the colon.

From considerations pertaining particularly to this species, it has seemed that both accuracy and simplicity require that the presence or absence of denticular serrations cease to be considered a cardinal key-character for the separation of species within this genus. Keys, such as those of Boulenger (1916), Theiler (1923), and Cram (1924), which separate these species into those with "teeth usually not denticulated" and those with "teeth usually denticulated" are of little assistance. At least, if this character be used, *T. minor* should be placed with the species having denticulated teeth rather than with those species with which it has been placed in the past. Moreover, in G. Theiler's monograph, which has contributed so significantly to our knowledge of equine helminths, it has seemed that for the plate which figures *T. minor* (p. 757, fig. A) she may have mistakenly drawn the anterior end of a male specimen of *T. brevicauda*. It is unlikely that female specimens

would permit of confusion, because of their conspicuously different posterior ends. Our specimens of *T. minor* are as figured by Ihle (1922a), the teeth, at least in most cases, being serrated, although not to so marked a degree as is usually observed in *T. tenuicollis*. These considerations are presented only with the object of minimizing the confusion which might arise among a well-standardized group of species as a result of a misleading key or a mislabeled drawing.

It appears that a simple and accurate key to these species, based upon the readily discernable characters which one familiar with these species unconsciously uses for their separation, might be constructed as follows:

Key to *Triodontophorus* species

1. Mouth-collar conspicuously circular in profile ..... *T. serratus*
   Mouth-collar not as above, but flattened marginally 2
2. Flattened edges of mouth-collar directed anteriorly; tail of female blunt; dorsal ray of bursa very long (625 microns) ..... *T. brevicauda*
   Characters not as above 3
3. Buccal capsule relatively small (124×85 microns); bursa short; body distinctly tapered anteriorly ..... *T. tenuicollis*
   Buccal capsule relatively large (160×135 microns); bursa long (525 microns); anterior end rather large and prominent ..... *T. minor*

There is only one element of difficulty which might arise in making identifications of the above species, namely, the distinction with certainty between females of *T. tenuicollis* and *T. minor,* which are very closely allied, and in this circumstance, we submit that the differences between the buccal capsules is the most reliable single criterion.

T. tenuicollis Boulenger, 1916

About one-fourth (27 per cent) of the animals of this series harbored this species. It was recovered from 9 horses (53 per cent) and 4 mules (13 per cent), a difference which may indicate a preference for the horse. Although only 42 specimens were recovered, these were taken mainly from the ventral colon (86 per cent) as opposed to the dorsal colon (14 per cent) which was considered by G. Theiler as the usual habitat of the species. Although 13 worms were (in one instance, taken at one autopsy, this species may be regarded as one of the rarer Strongylid species covered in this survey. Specimens were often encountered, 3 or 4 in a group, attached to a small ulcer, although, as was true also of *T. minor,* solitary specimens were not infrequently observed to be responsible for small ulcerations.

T. brevicauda Boulenger, 1916

This interesting species was taken upon 7 occasions (15 per cent) the proportions of horses and mules which were infested being about

equal. Although the maximum infestation was 5 worms, a total of only 16 specimens were found, 15 of which were from the ventral colon. It was not found in the cecum and was one of the least common of the Strongylid species.

Genus *Craterostomum* Boulenger, 1920

Craterostomum mucronatum (Ihle, 1920)

Two specimens of this species were taken from separate animals; one a horse, the other a mule. Both occurred in the dorsal colon.

Subfamily *Cyathostominae* Nicoll, 1927

This subfamily name became obligatory upon acceptance of the genus *Cyathostomum* Molin, 1861 (syn., *Trichonema* Cobbold, 1874, *Cylicostomum* Railliet, 1901, *Cylichnostomum* Looss, 1901). With the elevation of Ihle's (1922) subgenera [*Cylicostomum* (Railliet, 1901), *Cylicostephanus, Cylicocercus, Cylicocyclus, Cylicodontophorus, Cylicotetrapedon* (1925)] to generic rank and the addition of new genera by Cram (1924) (*Cylicotoichus, Cylicobrachytus*), the genus *Cyathostomum* becomes restricted to the *tetracanthum-coronatum* group of Looss (1901). It is then, as at present used, synonymous with the subgenus *Trichonema* (Cobbold, 1874) Yorke and Maplestone, 1926, and the subgenus *Cylicostomum* (Railliet, 1901) Ihle, 1922. The subfamily is synonymous with *Cylicostominae* Railliet, 1915, and *Trichoneminae* Railliet, 1916.

This subfamily was represented in this survey by 9 genera and 24 species, which accounted numerically for about six-sevenths of the Strongylid fauna, although many of the species, because of their relatively small size, are not particularly conspicuous. The *Cyathostominae,* except *Gyalocephalus,* are distinguished mainly by their ring-shaped or cylindrical buccal capsules and the relative proximity of anus and vulva.

Genus *Cyathostomum* Molin, 1861

Three species of this genus were found during this survey, one or more of which was encountered in 42 animals (88 per cent). Nine animals harbored only 1 species, 13 harbored 2 species, and 20 harbored all three. From 6 animals no species of this genus were recovered. No preference was indicated as to horse or mule host, except possibly in the case of *C. labratum,* the distribution of which is interesting because it appeared to favor slightly the mule host. All three species occurred in all three portions of the large bowel, although as shall be indicated, each of them demonstrated a definitely preferred habitat.

Cyathostomum coronatum Looss, 1900

This was the characteristic Cylicostome of the cecum, second only to *S. vulgaris* among the Strongylid species in its incidence and abundance in that region of the bowel. It was present in 39 cases (81 per cent), the proportions of horses and mules being about equal. The maximum infestation was 111 specimens, all from the cecum. For the animals harboring this species, the average number of worms was about 27, the minimum 1. Of a total of 1055 specimens, over 90 per cent were from the cecum, over 9 per cent from the ventral colon, and a negligible percentage from the dorsal colon. Among the Strongylid species, it was the 9th commonest.

C. labiatum (Looss, 1901)

About half of the horses and mules harbored this species. Of 1009 specimens, 99 per cent were from the ventral colon, the remainder scattered in both the cecum and dorsal colon. In its preferred localization it was the 5th commonest Strongylid species, although among all of the species it was 10th in rank of abundance. It may therefore be regarded as one of the commoner Cylicostomes.

C. labratum Looss, 1900

Although this species showed a lower average infestation (18) than *C. labiatum* (39), it was found more frequently (63 per cent) than the latter (54 per cent). The 30 animals harboring this species included 71 per cent of the mules and 47 per cent of the horses. In other respects, *C. labratum* paralleled very closely *C. labiatum,* discussed above.

Genus *Gyalocephalus* Looss, 1900

Gyalocephalus capitatus Looss, 1900

Seven specimens of this species were recovered from the ventral colon of horses upon four occasions. It was not found in mules nor in any region other than that named. The largest number recovered from one animal was 3.

Genus *Poteriostomum* Quiel, 1919

Twenty-two animals (46 per cent) harbored species of this genus. Five were positive for both species and 17 harbored either one or the other. On the whole, these parasites were rather rare, although both species were taken from both hosts. They showed a distinct preference for the dorsal colon.

Poteriostomum imparidentatum Quiel, 1919

This species, 18th in rank among the Strongylid fauna, was taken from both horses (29 per cent) and mules (16 per cent) upon 10

occasions (21 per cent). A total of 64 specimens were taken, all from the dorsal colon, where the heaviest infestation was 28 worms. It was the 8th commonest form of the dorsal colon among the specimens recovered during this survey.

P. ratzii (Kotlán, 1919)

Although this species occurred more often (35 per cent) than the above, and showed a higher incident (59 per cent) in the horse than in the mule (22 per cent), it was much less numerous. Only 35 specimens were recovered, all but one of which were from the dorsal colon, where the largest single infestation was 8 worms. It was 21st in rank among the *Strongylidae*.

It has been interesting to find that these specimens of *P. ratzii* conform closely to *P. ratzii* var. *nanum* Theiler, 1923, particularly in respect to the arrangement and structure of the bursal rays. In particular, our specimens uniformly lacked the characteristic thumb-like process of the dorso-lateral way which is ascribed to the typical species, and which we have regularly observed in *P. imparidentatum*. Males varied from 10 to 13 mm. in length, and females 10.5 to 18 mm. The diameter of the buccal capsule was 174 to 201 microns and its depth 53 to 67 microns. The mouth-collar varied greatly in height. It is apparent from these data that in respect to the bursa and the size of the specimens, there is a close approach to Theiler's variety, yet the measurements of the buccal capsule, particularly the depth, approach more clearly the typical species. Moreover, there is considerable variability among specimens of both species of this genus, a consideration which supports Skladnik's view that Theiler's variety may be best considered a synonym of *P. ratzii*. This leaves but two species within the genus, the simplest key to which is as follows:

Key to *Poteriostomum* species

1. Elements of internal leaf-crown of unequal length ..... *P. imparidentatum*
   All elements of same length ..... *P. ratzii*

Genus *Cylicobrachytus* Cram, 1924

Cylicobrachytus brevicapulatus (Ihle, 1920)

The analysis of the data upon this species as to its rank, occurrence, distribution, and other factors and even in respect to the sex of the specimens (female) has shown it to be exactly parallel, in these respects, to *Craterostomum mucronatum*, discussed above. The only possible exception to this statement is that *C. brevicapsulatus* was found only in the horse (on but 2 occasions) while the former species was taken once from each host.

Although of rare occurrence, this species seems to be sufficiently distinct from all others to be readily recognizable when found. It is conspicuous microscopically by virtue of its relatively large size, prominent external leaf-crown, short buccal capsule, and thick, characteristically-shaped, oesophagus. This worm has apparently been found only twice before, and these occasions were by workers who examined a large number of animals. It was described by Ihle (1920) who recovered it from one horse in Holland. Later G. Theiler (1923) came upon one female specimen which had been taken from the pelvic flexure of a horse in South Africa. It is unfortunate that the absence of male specimens precludes, for the present, further comment upon the status of this species.

Genus *Cylicocercus* Ihle, 1922

Three species of this genus were recovered abundantly during this survey. These did not, however, include the type species, *C. alveatus* (Looss, 1900). It has been of some interest to note that in reports of equine species from Holland (Ihle, 1922a), Porto Rico (McIntosh, 1933), and Poland (Skladnik, 1935a), this species was also absent, while the other three species of the genus were listed. Other than the relatively numerous reports of *C. alveatus* from various parts of Africa (Looss 1901, Gough 1908, Yorke and Macfie 1920, Boulenger 1920, Theiler 1923) this species is either uncommon or it does not enjoy the widespread distribution which is so characteristic of most of the equine fauna. It has been noted by others (i.e., Theiler) that *Cyathostomum tetracanthum* (of Looss) is also somewhat peculiar in these respects.

In spite of what has been said, the genus *Cylicocercus* was among the most abundantly represented of the Strongylid genera, as about 13 per cent of the specimens were assigned to this genus. Every animal harbored at least one species of this genus. Over half of them (26) harbored all three species, while 15 harbored two (and only 2) species, and 7 animals only 1 species each. There was no indication of a preference for either the horse or mule host by any of the 3 species.

Cylicocercus catinatus (Looss, 1900)

This species was recovered from 43 animals (90 per cent) which number included all of the horses and 26 (85 per cent) of the mules. The maximum infestation was 897 worms, all of which, in this instance, were from the ventral colon. Although this region is undoubtedly the preferred habitat of this species, since over 96 per cent of the specimens were recovered from it, it is also true that, during this survey, this species was recovered from all three parts of the large bowel. Roughly 4 per cent of the specimens were divided about equally between the

cecum and dorsal colon. *C. catinatus* was the commonest species of the genus, and the sixth commonest among the Strongylid species. It was, however, the 4th commonest species in its preferred habitat, the 5th commonest from the dorsal colon, and the 6th from the cecum.

We have followed Skladnik (*loc. cit.*) in his synonymy of the varieties of this species with the typical form, although it has appeared that the majority of our specimens conform to *C. catinatus* var. *pseudocatinatus* (Yorke and Macfie, 1919).

C. goldi (Boulenger, 1917)

This is a characteristic species of the dorsal colon. As in the case of *C. catinatus* this form occurred in 43 animals. Of these, 16 (94 per cent) were horses and 27 (87 per cent) were mules. Of a total of 1509 specimens, 99 per cent were from the dorsal colon and about 1 per cent from the ventral colon. It occurred infrequently in the cecum also. It is remarkable that upon two occasions, a single adult specimen of *C. goldi* was recovered from the stomach, these being the only instances in which any of the Strongylid fauna were found outside of the large bowel. On the basis of our data, this was the 8th in abundance among the Strongylid species, and the 3rd commonest in its preferred habitat.

C. pateratus (Yorke and Macfie, 1919)

Twenty-nine animals (61 per cent) harbored this species. Unlike the other species *C. pateratus* occurred more frequently in mules (68 per cent) than in horses (47 per cent), although this is probably not indicative of a host-preference, since a large proportion of both hosts were infested. The distribution of specimens within the large bowel was quantiatively the same as given above for *C. goldi* with the important difference that *C. pateratus* was almost entirely restricted to the ventral colon instead of the dorsal. It was among the least common (13th in rank) among the species from both the cecum and dorsal colon, although it was the 6th commonest of the ventral colon fauna, and the 11th among the species of *Strongylidae*.

Genus *Cylicodontophorus* Ihle, 1922

On the whole, species of this genus were of rather uniformly infrequent occurrence, since the entire genus was represented in this survey by only 48 worms, although these were assignable to three species, each showing about the same incidence. Thirty-four animals (71 per cent) were apparently negative for species of this genus. Ten were infested with only one species, although 3 had double infections, and 1 harbored all three of the species.

Cylicondontophorus euproctus (Boulenger, 1917)

Six horses harbored this species in the dorsal colon. Although 11 specimens were taken from one animal, only 30 specimens in all were recovered. Over one-third of the horses harbored *C. euproctus,* yet it was not found in mules nor was it taken from any region other than the dorsal colon. Of the fauna characterizing this habitat, this was the 11th commonest species.

C. bicoronatus (Looss, 1900)

This species, taken from the ventral colon in each case, was recovered from 7 animals (15 per cent) including both hosts. Only 9 specimens were taken, the most from one animal being 3. Six animals harbored one specimen each. This was one of the least common of the Strongylid species recovered during the survey.

C. ultrajectinus (Ihle, 1920)

Nine specimens of this species were taken from 6 animals (13 per cent) including both hosts. All were found in the dorsal colon.

This species, which often has been observed in animals other than those included in this survey, is thick and fat and readily recognized at autopsy because of its characteristic sluggishness and distinct color, which is a kind of mottled gray.

Genus *Cylicostephanus* Ihle, 1922

Five species of this genus, 3 quite common and 2 relatively rare, were recovered from the equines of this survey. One animal harbored all five species, 5 harbored 4 species, 26 harbored 3 species, 12 two species each, and 4 only one species each. None were without representatives of this genus. In these five species are contained typical species of each part of the large bowel and there was no indication of a host-preference in any case.

Cylicostephanus calicatus (Looss, 1900)

This worm was 3rd in abundance and 6th in incidence among the Strongylid fauna reported in this paper. It occurred about equally among horses (76 per cent) and mules (84 per cent), and was taken from 39 (81 per cent) animals in all. The largest number taken from one animal was 924. The total number of specimens recovered and identified from the animals of this series (5388) were distributed about as follows; from the ventral colon, 94 per cent, from the cecum 5 per cent, and dorsal colon 1 per cent. It was the 2nd commonest species of the genus, and the 2nd in rank among the *Strongylidae* of the ventral colon. It was also the 4th most abundant species of the cecum, and the 6th of the dorsal colon.

At autopsy, this species because of its delicate size and the color which it sometimes exhibits, has often appeared to resemble a short strand of black thread.

C. poculatus (Looss, 1900)

This species has apparently been reported previously only from the horse. In this locality we have several times recovered it from mules and in the present series of animals it was taken from 3 horses and 1 mule, always from the cecum. Only 11 specimens were recovered, 7 of which were from one animal.

C. minutus (Yorke and Macfie, 1918)

This delicate and appropriately named worm was among the commonest of the Cylicostomes, occurring regularly in both horses and mules. Ninety-eight per cent of the specimens were taken from the ventral colon while the rest were distributed about equally between the cecum and dorsal colon. It was the 5th commonest Strongylid species, and next in abundance to *C. calicaus* in its preferred localization.

C. longibursatus (Yorke and Macfie, 1918)

Next to *S. vulgaris* this was the most frequently occurring Strongylid species and after *C. nassatus* (to be discussed later) it was the most abundant. Although specimens were taken from all three parts of the large bowel, 98 per cent were from the dorsal colon, where it was easily the predominant species. It was taken very infrequently from the cecum. The infected animals included all of the horses and all but 2 of the mules. The largest number from one animal, although more were probably present, was 1015.

C. hybridus (Kotlán, 1920)

This species was taken from 3 horses and 2 mules. Of a total of 46 specimens, 37 were from one animal. It did not occur in the dorsal colon but 96 per cent of the specimens were from the ventral colon. According to our data, this species was the 17th commonest in the ventral colon and the 12th of the cecum. On the whole it was one of the rarer species, ranking 19th among the Strongylid fauna.

Genus *Cylicotetrapedon* Ihle, 1925

This genus was created to include *Cylicostomum bidentatum* Ihle, 1925, and *C. asymetricum* Theiler, 1923, which species are distinct from others by nature of an asymmetry in the depth of their buccal capsules and by the fact that the buccal walls are thicker anteriorly than posteriorly. It is questionable whether these differences should be given

generic significance, particularly since there is nothing to exclude these species from the genus *Cylicostephanus,* already discussed. Moreover, it is felt that Cram was perfectly correct in pointing out that the elevation of Ihle's subgenera to genera serves, in the main, only to "simplify matters." One might well contend that for this reason also the above genus should be dropped, a view which has become even more reasonable since Skladnik (1935) has synomymized Ihle's species with *C. asymetricum,* leaving only one species within the genus. Moreover, Theiler originally placed *C. asymetricum* with the *calcatum-longibursatum* group which has been considered above under the genus *Cylicostephanus.* For the present, however, we shall accept this species as a member of an independent genus.

Cylicotetrapedon asymetricum (Theiler, 1923)

There were found two specimens of this species, one from the ventral colon of a mule, the other from the dorsal colon of a horse.

Of this species G. Theiler recovered 11 specimens from the ventral colon and 26 from the dorsal (considering the pelvic flexure as a part of the dorsal colon), in consequence of which she regarded this worm as probably a predominantly dorsal colon form. It is interesting that one is inclined to accept tentatively this viewpoint because of the fact that the dorsal colon is spectacularly the habitat of most of the very rare species (i.e., *C. mucronatum, O. robustus, C. brevicapsulatus, C. euproctus, C. ultrajectinus,* etc.). It has seemed that the observation that rare forms are predominantly dorsal-colon species can scarcely be questioned, although it would, of course, be folly to reason, in the light of our present knowledge, that this is anything but a coincidence.

Genus *Cylicocyclus* Ihle, 1922

Five species of this genus were recovered. Six animals harbored no representatives and none harbored all five. Eight were infested with one species each, 13 with two species, 15 with three, and 6 with four each. There were no host-preferences indicated.

Cylicocyclus radiatus (Looss, 1900)

This species was relatively rare, only 26 specimens having been taken from 7 animals. They were mainly from the ventral colon (96 per cent), although a few occurred in the dorsal colon (4 per cent). Twelve was the largest number taken from one animal.

C. elongatus (Looss, 1900)

Seven specimens were taken from 5 animals, 2 were from the cecum, 4 from the ventral colon, and 1 from the dorsal colon.

Theiler records this species as a "characteristic form of the cecum of the donkey, rarely occurring elsewhere." It may be permissible to remark that, although this species was among the rarest covered in this survey, it has been observed to be a common parasite of native interior animals (horses and mules) of Panama. Its characteristic habitat is the cecum, although, as among the present series, it may be found in any portion of the large bowel.

Our specimens are all of the var. *kotláni* (Ihle, 1920), although we have followed Skladnik's (1935a) apparently sound synonymy of this variety with the typical form.

C. nassatus (Looss, 1900)

This was the most abundant of the Strongylid species, in itself accounting for nearly one-fifth of the total Strongylid fauna. It occurred in 40 animals (83 per cent) and in all three parts of the large bowel of both the horse and mule hosts. It did, however, show a 94 per cent concentration within the ventral colon, where it was the commonest species. It was, however, also common in both the cecum and dorsal colon, such that, in spite of its preferred habitat, this species must be regarded as typical of the fauna from each of the three regions. The largest number of worms recovered and identified from one animal was 1689, and the total 7677.

Our specimens were of the var. *parvus* (Yorke and Macfie, 1918), although we have accepted, in this case also, the synonymy of Skladnik (*loc. cit.*). Male specimens were 7.5 to 8 mm. and females 9.2 to 11 mm. in length.

C. insigne (Boulenger, 1917)

This was one of the characteristic species of the dorsal colon, although it occurred rarely in the ventral colon and very infrequently in the cecum. Thirty-one animals (65 per cent) harbored this species, the largest single infestation being 561 worms. It was the 7th commonest of the Strongylid fauna but second only to *C. longibursatus* in the dorsal colon.

This species, when present, is very conspicuous, not only because of its larger size compared to the other Cylicostomes of the dorsal colon, but also because of the brilliant red color which is so characteristic of the young adult specimens.

C. leptostomus (Kotlán, 1920)

In many respects, this was a borderline species, being neither common nor rare. Twenty animals (42 per cent) harbored this worm, although only 180 specimens, in all, were recovered. The maximum infes-

tation was 44. It was 16th in abundance and 14th in incidence of the Strongylid fauna and was encountered in all three portions of the large bowel, although 96 per cent of the specimens were from the ventral colon, where it was the 10th most abundant species.

Suborder *Oxyurata* Cram, 1927

Superfamily *Oxyuroidea* Railliet, 1916

Family *Oxyuridae* Cobbold, 1864

Two rather distantly related species of Oxyurids were recovered quite commonly from the equines of this series.

Genus *Oxyuris* Rudolphi, 1803

Oxyuris equi (Schrank, 1788)

This species was not abundant in these animals. Small numbers of adult worms, fourth-stage larvae, and transitional stages were recovered from 18 animals (38 per cent). Twelve of the positive animals were horses (71 per cent) and 6 were mules (19 per cent). It is possible that this difference in incidence between horses and mules may indicate a preference for the horse-host. The numbers of adult worms varied from 2 to 297 per animal. Male specimens were plentiful, when the parasite was present. The dorsal colon and the terminal portions of the intestinal tract were the regions normally infested. Although no attempt was made to study quantitatively the larval and transitional stages, it was noted that these were usually much more numerous than adults and that they occurred typically in the dorsal colon. All stages occurred infrequently in the ventral colon, and even in the cecum.

In an otherwise splendid study upon the biology of the fourth stage larvae, Wetzel (1930) has stated that in the 17 fresh autopsies observed by him, these larvae were "always attached to the mucous membrane" and "always restricted to the ventral colon" (p. 95). On the basis of my own observations, I am impelled to state that these larvae were sometimes or (less conservatively) often attached to the mucous membrane and nearly always most abundant in the dorsal colon.

Genus *Probstmayria* Ransom, 1907

Probstmayria vivipara (Probstmayr, 1865)

The very small size of this species precluded from the start any attempt to study its occurrence quantitatively. There was, indeed, no attempt made to examine for the presence of this species at autopsy. Our data are, however, of such a nature as to throw considerable light, conservatively, upon the occurrence, abundance, and localization of this

scarcely visible species. In the collection of Strongylid species, as described previously, it will be recalled that specimens from the cecum, ventral colon, and dorsal colon, respectively, were collected into bottles of normal salt solution. Upon returning to the laboratory the content of each bottle was emptied and rinsed into a large glass Petri dish prior to fixing the worms. After all of the helminths were removed, the solution was routinely examined under the low-power of the microscope for specimens which had escaped the eye and to determine the presence of *P. vivipara.* More often than not that part which had contained the worms from the ventral colon was abundantly supplied with specimens of *P. vivipara.* These were neither counted nor saved, except for a few hundred specimens which have been kept in our collection. In other words, specimens of *P. vivipara* were apparently so numerous, when present, as to have been collected in large numbers, probably adhering, for the most part, to larger species.

Our records show that this species was found after this manner in 27 animals (56 per cent) including 8 horses (47 per cent) and 19 mules (61 per cent). They were taken from both the cecum and dorsal colon, but were typically abundant in the collections from the ventral colon. In more than half the cases, they were observed only from this region. It may be concluded then, that this is a very common species, at least in this locality. In abundance, it can scarcely be questioned that, could quantitative studies be made on this species, it would be many times more numerous than any of the other equine species. To consider this species rare, as has been frequently indicated in the literature, is to be misled by its insignificant size.

Suborder *Ascaridata* Railliet and Henry, 1915

Superfamily *Ascaroidea* Railliet and Henry, 1915

Family *Ascaridae* Baird, 1853

Genus *Parascaris* Yorke and Maplestone, 1926

Parascaris equorum (Goeze, 1782)

This species was uncommon among the equines of this series. Three horses and six mules were infested, practically all of the worms being immature. The number per animal varied from 2 to 14. Although this species localizes mainly in the upper part of the small intestine, three specimens were, in one case, taken from the stomach.

Suborder *Spirurata* Railliet and Henry, 1915

Superfamily *Spiruroidea* Railliet and Henry, 1915

Family *Spiruridae* Oerley, 1885

Genus *Habronema* Diesing, 1861

Three species of this genus were of rather common occurrence during this survey. Thirty-five animals (73 per cent) were infested. Three harbored all three species, 18 harbored 2 species, and 14 harbored only one species. Because of the intimate association of these species with the gastric mucosa, there is in every case some doubt as to the thoroughness with which the worms were collected. It is not felt that our data approach the actual infestations of these animals, although it was apparent that, in general, the infestations were relatively light. Moreover, the data are sufficiently reliable to show roughly the incidence and relative abundance of each species.

Habronema muscae (Carter, 1861)

This species was recovered from 30 animals (63 per cent), including 12 horses (71 per cent) and 18 mules (58 per cent). The number per animal ranged from 1 to 106. It was not unusual to recover this species from the surface of the content-mass from the stomach, although more often the worms were buried in the mucous exudate of the stomach tissue.

H. megastoma (Rudolphi, 1819)

Although of lower incidence than either of the other species of the genus, *H. megastoma* is probably the most important pathogen. From 4 to 20 worms per animal were taken upon six occasions from walnut-sized gastric tumor-like abscesses, always showing a sanguinous aspect, and generally located upon the margin of the cardiac glandular region of the mucosa. In comparison with our observations upon native animals, where several hundred worms have been taken from a single abscess, it may be permissible to consider that the infestations among the animals of this series were very light.

H. microstoma (Schneider, 1866)

This was the most abundant species of the genus although it occurred less often than *H. muscae*. It was found in 22 animals (46 per cent), the number of specimens varying from 1 to 127 per animal, and was observed to be associated at times with an eroded and ulcerated mucosa. It is particularly interesting that this species was taken from 61 per cent of the mules (19) and only 18 per cent of the horses (3). Considering that these animals were raised under the same conditions, one is prompted to suggest that of the two, perhaps the mule is the more natural host for this species.

Superfamily *Filarioidea* (Weinland, 1858) Stiles, 1907

Family *Filariidae* (Cobbold, 1864) Claus, 1885

Genus *Setaria* Viborg, 1795

Setaria equina (Abildgaard, 1789)

Nine animals (19 per cent) harbored this species in the body cavity. From each of 2 horses and 7 mules, from 1 to 4 specimens were taken.

DISCUSSION

Species encountered.

From the 48 horses and mules covered by this survey there are recorded, in addition to the Cestode species, *Anoplocephala perfoliata,* which is mentioned in the introductory pages, a total of 39 different Nematode species. Of these, 32 species were of the family *Strongylidae* and their generic distribution as follows: *Strongylus* 3, *Triodontophorus* 4, *Craterostomum* 1, *Cyathostomum* 3, *Gyalocephalus* 1, *Poteriostomum* 2, *Cylicobrachytus* 1, *Cylicocercus* 3, *Cylicodontophorus* 3, *Cylicostephanus* 5, *Cylicotetrapedon* 1, *Cylicocyclus* 5. The seven other species, not closely related systematically, were *Oxyuris equi, Probstmayria vivipara, Parascaris equorum, Habronema muscae, H. megastoma, H. microstoma,* and *Setaria equina.*.

Host-variations in the number of different species and their abundance.

In the animals of this series the number of different species of *Strongylidae* varied from 6 to 22 per animal, with an average of 15. In the cecum the number of different species ranged from 2 to 9, with an average of 5. For the ventral colon, the variation was from 3 to 16, averaging 11. The dorsal colon showed a range of from 1 to 14 different Strongylid species, with an average of 6.

The total number of Strongylid worms recovered from these animals varied from 36 to 4124 and averaged 849 per host. In the cecum the range was from 2 to 354, with an average of 127. The range from the ventral colon was from 9 to 3765 worms, with an average of 486. For the dorsal colon the range was from 2 to 1121 worms, with an average of 236 per animal.

Of the 7 species, other than *Strongylidae,* these animals harbored from none to 5 species each, and averaged 2 to 3 species (2.56) per animal. Considering, as a group, these extra-*Strongylidae,* it may be summarized that 1 animal harbored none of these species, 8 harbored 1 species, 17 harbored 2 species, 9 harbored 3 species, 11 harbored 4 species, and 2 harbored 5 species.

With respect to the numerical importance of these extra-*Strongylidae,* our data show an average, per animal, of about 33 worms each, exclusive of *P. vivipara* and fourth stage larvae of *O. equi.*

Relative abundance of different species of Strongylidae.

A total of 40,707 Strongylid parasites were identified from these equines, of which 40,145 or 98.62 per cent were accounted for by 15 species. These were also the more frequently occurring species, as will be indicated, and it will be recalled that 15 was also the average number of different Strrongylid species per animal. Also from what has been said above, it follows that 17 of the 32 species accounted for less than 1.5 per cent of the total Strongylid fauna. Consequently, in respect to their abundance, the Strongylid species fall readily into two groups which have been conveniently designated as the "commoner" and "rarer" species. These species and their abundance, together with a summary of data upon their localization and incidence, are presented in Table 1.

This table gives the rank, in abundance, of each species and the data from which these positions were determined. In order to facilitate comparisons, percentages have been employed to indicate the distribution of the specimens of each species although the ranks representing the relative abundance of the several species from the different regions have, of course, been determined from the actual numbers of worms.

In order to avoid unnecessary repetitions of specific names and comparative data, there have also been included in Table 1, certain information which shall be utilized in later discussions.

It may be observed, in addition to what has already been said about the abundance of species, that a large proportion of the Strongylid fauna is accounted for by relatively few of the commonest species. For example, *C. nassatus,* constituted about 1/5 of this fauna. This species and *C. longibursatus,* together, accounted for about one third. These two and *C. calicatus* represented about ½, and, proceeding further, it has been calculated that less than 1/5 of the Strongylid species (the 6 commonest) accounted for about 4/5 of the fauna.

Incidence of species

Of the *Strongylidae,* it may be observed in Table 1 that 15 species, coinciding exactly with the 15 more abundant species, were taken from more than half of the animals, while 17 were taken from less than half. Moreover, 11 of these "commoner' species occured in over three-fourths of these equines, while 13 of the "rarer" species occurred in less than one-fourth. Every species occurred at least twice, although only two specimens each were recovered of *C. mucronatum, C. brevicapsulatus* and *C. asymetricum.*

TABLE I.—*An arrangement of the species of Strongylidae in the order of their abundance, giving comparative data upon their localization and incidence*

Species	Abundance		Localization						Preferred Habitat	Incidence				
			Cecum		Ventral C.		Dorsal C.							
	No. Spec.	Rank	%	Rank	%	Rank	%	Rank		No. Pos.	Rank	% Pos.	Horses Pos. (%)	Mules Pos. (%)
The "commoner" species														
Cylicocyclus nassatus	7677	1	5	3	94	1	1	4	VC	40	5	83	82	84
Cylicostephanus longibursatus	7178	2	+	12	2	12	98	1	DC	46	2	96	100	95
C. calicatus	5388	3	5	4	94	2	1	6	VC	39	6	81	76	84
Strongylus vulgaris	4200	4	96	1	3	11	1	12	C	48	1	100	100	100
Cylicostephanus minutus	3933	5	1	7	98	3	1	9	VC	37	7	77	71	81
Cylicocercus catinatus	3095	6	2	6	96	4	2	5	VC	43	3	90	100	84
Cylicocyclus insigne	2272	7	+	11	4	15	96	2	DC	31	9	65	65	64
Cylicocercus goldi	1509	8	+	13	1	22	99	3	DC	43	3	90	94	87
Cyathostomum coronatum	1055	9	91	2	9	13	+	17	C	39	6	81	82	81
C. labiatum	1009	10	+	12	99	5	1	15	VC	26	12	54	53	55
Cylicocercus pateratus	848	11	+	13	99	6	1	13	VC	29	11	61	47	68
Triodontophorus minor	668	12	..		89	7	11	7	VC	32	8	81	100	71
Cyathostomum labratum	543	13	1	10	97	8	2	14	VC	30	10	63	47	71
Strongylus edentatus	430	14	15	6	84	9	1	17	VC	41	4	85	94	81
S. equinus	340	15	72	5	27	14	1	21	C	41	4	85	88	84
The "rarer" species														
Cylicocyclus leptostomus	180	16	2	11	96	10	2	17	VC	20	14	42	35	46
Triodontophorus serratus	74	17	37	8	63	16	...	–	VC	22	13	46	88	22
Poteriostomum imparidentatum	64	18	...	–	...	–	100	8	DC	10	17	21	29	16
Cylicostephanus hybridus	46	19	4	12	96	17	...	–	VC	5	20	10	18	6
Triodontophorus tenuicollis	42	20	...	–	86	18	14	16	VC	13	16	27	53	13
Poteriostomum ratzii	35	21	...	–	3	25	97	10	DC	17	15	35	59	22
Cylicodontophorus euproctus	30	22	...	–	...	–	100	11	DC	6	19	13	35	...
Cylicocyclus radiatus	26	23	...	–	96	19	4	19	VC	7	18	15	24	10
Triodontophorus brevicauda	16	24	...	–	94	20	6	19	VC	7	18	15	12	16
Cylicostephanus poculatus	11	25	100	9	...	–	...	–	C	4	21	8	18	3
Cylicodontophorus bicoronatus	9	26	...	–	100	21	...	–	VC	7	18	15	18	13
C. ultrajectinus	9	26	...	–	...	–	100	15	DC	6	19	13	24	6
Gyalocephalus capitatus	7	27	...	–	100	23	...	–	VC	4	21	8	24	...
Cyliocyclus elongatus	7	27	29	12	57	24	14	19	..	5	20	10	12	10
Craterostomum mucronatum	2	28	...	–	...	–	100	18	DC	2	22	4	6	3
Cylicobrachytus brevicapsulatus	2	28	...	–	...	–	100	18	DC	2	22	4	12	...
Cylicotetrapedon asymetricum	2	28	...	–	50	25	50	19	..	2	22	4	6	3

Of the extra-*Strongylidae,* none were rare, although only the stomach worms as a group (*Habronema* spp.) and *P. vivipara* may be considered to have been common.

Host-preferences.

Our observations have indicated that, in general, both horses and mules are good natural hosts for the majority of the species encountered. There were, however, 3 species which were found only in horses; viz., *G. capitatus, C. brevicapsulatus,* and *C. euproctus.* Also three of the *Triodontophorus* species (excepting *T. brevicauda*) and *P. ratzii* were recovered from a significantly greater percentage of horses than mules. No species were found exclusively in mules, although *C. labratum* showed a slightly greater incidence in this host.

Of the extra-*Strongylidae,* it appears that the horse was the slightly favored host by *O. equi* while *H. microstoma* was found in a much larger percentage of mules than horses.

Host-localization of Strongylid species.

Eight species (one fourth of the total) were recovered exclusively from one region of the large bowel. *C. poculatus* was found only in the cecum, *G. capitatus* and *C. bicoronatus* only in the ventral colon, and *C. mucronatum, P. imparidentatum, C. brevicapsulatus, C. euproctus,* and *C. ultrajectinus* only from the dorsal colon. Eight other species (another fourth) were taken only from two adjoining portions of the large bowel. By reference to Table 1, it may be noted that *T. serratus* and *C. hybridus* were taken from both the cecum and ventral colon. Similarly, 3 *Triodontophorus* species, *P. ratzii, C. asymetricum,* and *C. radiatus* were each taken from both the ventral and dorsal colon, but never from the cecum. The other 16 species, exactly half, and including most of the "commoner" ones, occurred at one time or another in all three regions. These considerations, although interesting, do not, however, emphasize adequately the extent to which the several species were observed to be localized in a single region. In 25 of the 32 species, more than 90 per cent of the specimens were concentrated in a single part of the bowel. Moreover, available data indicate that for *every* species there is a preferred or normal localization. There are two instances where our data, by reason of their insufficiency, may be misleading, hence attention is called to them at this point. During this survey, *C. elongatus* occurred but rarely, and only 7 specimens were taken. Their distribution indicated that this species may occur in any part of the bowel, although, contrary to the possible implication of our data, this form, as noted by others (e.g., Theiler) and as observed by us in autopsies of native animals, is essentially a cecal form. In the

other instance, *C. asymetricum,* as mentioned earlier, is probably a dorsal colon species, although during this survey, it was taken once from the dorsal colon and once from the ventral colon.

To summarize further, Table 1 shows that a total of 19 different species occurred, at one time or another in the cecum, that 26 occurred in the ventral colon, and that 27 different species were taken from the dorsal colon. Conversely, it follows that 13 species were not found at any time in the cecum, that 6 species did not occur in the ventral colon, and that 5 never were taken from the dorsal colon. It is usually considered that the ventral colon shows the greatest variety and abundance of fauna, an observation which, in general, is further emphasized by these data, yet when one considers the chance-occurrence of the "rarer" species, it becomes apparent that the dorsal colon has potentially as great a variety of fauna as does the ventral colon. This consideration comes from the fact, mentioned earlier, that the dorsal colon seems to be the remarkable habitat of so many of the "rarer" species. Of the "commoner" species, only 3 are characteristically dorsal colon forms, while of the "rarer" species, there are 7 which enjoy this distinction. The *average* animal, however, showed about twice as many different species in the ventral colon as elsewhere.

Although the data which have been presented, by reason of their quantitative character, leave no doubt that there is a definitely preferred habitat for each of the Strongylid species, there is an additional consideration which ought to be emphasized at this point since it gives even stronger support to these data. Often it has been observed that specimens encountered in regions other than the usual habitat for the species were immature adults or transitional larvae. The counts of such specimens, although relatively few in number, have been included in our data. Frequently, also, larvae and transitional stages of such species as *S. vulgaris, C. calicatus,* and *C. insigne* have been removed from soft nodules of the mucosa and submucosa of regions other than the preferred habitats for these species. Boulenger (1921) noted that *C. insigne* was mainly confined to the posterior colon, an observation which is thoroughly confirmed by our findings, but he noted, in addition, that larvae of this species occurred in the submucosa of the cecum. In keeping with this observation, it has been interesting to find during the present study, that most of the specimens of this species taken from either the cecum or ventral colon were very young adults or transitional larvae. It is true, of course, that these younger stages were also encountered in the dorsal colon, but it has seemed that the absence of the occurrence elsewhere of a proportionate number of adult specimens is significant. It seems very likely that a condition of larval development, paralleling Boulenger's observation in the case of *C. insigne,* may

be equally true of a number of other species. Such findings suggest that the larval stages of some of these species, or possibly all, may be passed in any region of the bowel, and that, after the emergence of the young adults into the lumen of the bowel, there is a migration to that region which one conveniently may call the "preferred habitat." There is need of much investigation along this line, although it has seemed that the facts thus far point to a distinct tendency, on the part of the adult worms of many species to localize in a single region of the bowel. This probably does not apply to certain of the very common species which, in spite of their quantitative concentrations, may be considered as typical of any region of the bowel.

The hypothetical infestation.

In view of what has been said, and in keeping with a desire to present a comprehensive picture of the verminous infestations of these equines, it has seemed natural that one should construct, using average figures of the actual data, an infestation which would represent, concisely and summarily, the findings of this survey. It has been stated that the average number of Strongylid parasites per animal was 849, and that the average in the cecum was 127, in the ventral colon 486, and in the dorsal colon 236. These figures represent the numbers of worms and their distribution which must be assigned to the hypothetical infestation. Moreover, the average number of different Strongylid species per animal was 15, and the average from the cecum was 5, from the ventral colon 11, and from the dorsal colon 6. These figures represent the number and distribution of different species which must be assigned to the hypothetical animal. The selection of the actual species to be assigned to this infestation is not more difficult. One has only to select, from Table 1, the 5 commonest species of the cecum, the 11 commonest from the ventral colon, and the 6 commonest from the dorsal colon. It is apparent from the averages given above that there must be a certain amount of "overlapping" of species, but since this represents precisely the situation which one encounters at every autopsy, there is no difficulty in the selection of these species. In order to determine the quantitative occurrence of the respective species, it is necessary only to divide the total number of specimens of each, taken from the respective regions to which they are assigned in the hypothetical infestation, by the number of animals covered in this survey. In other words, these also are average figures.

In view of these considerations, and since the data from which this infestation is derived are given fully in either the table or discussion, it may be permissible to present, without further comment, this average or so-called "hypothetical" infestation.

The hypothetical infestation

1. Number and distribution of Strongylid parasites.

Total		
849		
Cecum	Ventral colon	Dorsal colon
127	486	236

2. Number and distribution of different species.

Total		
15		
Cecum	Ventral colon	Dorsal colon
5	11	6

3. Hypothetical species, abundance of each, and their localizations.

Cecum		Ventral colon		Dorsal colon	
85	*Strongylus vulgaris*	151	*Cylicocylus nassatus*	147	*Cylicostephanus longibursatus*
20	*Cyathostomum coronatum*	105	*Cylicostephanus calicatus*	46	*Cylicocyclus insigne*
7	*Cylicicyclus nassatus*	81	*C. minutus*	32	*Cylicocercus goldi*
6	*Cylicostephanus calicatus*	62	*Cylicocerus catinatus*	2	*Cylicocyclus nassatus*
5	*Strongylus equinus*	21	*Cyathostomum labiatum*	2	*Cylicocerus catinatus*
		18	*Cylicocercus pateratus*	2	*Cylicostephanus calicatus*
123		13	*Triodontophorus minor*	231	
		11	*Cyathostomum labratum*		
		8	*Strongylus edentatus*		
		3	*S. vulgaris*		
		3	*Cylicostephanus longibursatus*		
		476			

To make the picture complete, one must add some 33 worms representing 2 species of extra-*Strongylidae,* say, for example, *Habronema muscae* and *Oxyuris equi,* and, in addition, *Probstmayria vivipara,* which was present more often than not.

Considering the manner in which this hypothetical infestation has been derived, it is remarkable that there appears in it only one item which may possibly be considered at variance with the actual data. In Table 1, it can be noted that *Cylicocyclus leptostomus,* a "rarer" species and predominantly localized in the ventral colon when it occurs, was 10th in abundance from this region. In the hypothetical infestation this species does not appear, although the two species (*S. vulgaris* and *C. longibursatus*) which ranked 11th and 12th respectively, do appear. These ranks were, of course, determined from the actual occurrence of these species in this region, the data being as follows; *C. leptostomus* 173, *S. vulgaris* 139, and *C. longibursatus* 120. In all, however, only

180 specimens were taken of the first-named species. It has been felt that, in the first place, these actual differences are not significant (considering the number of animals) and, in the second place, that there are many other reasons, including the fact that the hypothetical infestation was limited to a total of 15 *different* Strongylid species, which, upon consideration, more than justified the selections which have been made.

Finally, there are two further considerations which should be emphasized. In the first place, the quantitative occurrence of the respective species does not equal numerically the total number of worms postulated for the hypothetical imfestation. It does, however, approximate this number within 2 per cent, which is in remarkable agreement with the actual findings, in respect to which it has been pointed out that about 98 per cent of the Strongylid fauna was contained within the 15 commonest species—precisely the species listed in the hypothetical infestation. From this it becomes apparent that an allowance of 19 worms, or 2 per cent, for the occurrence of the "rarer" species, is not only in conformity with the data but is the most accurate postulation of what one might anticipate at autopsy. In the second place, the figures given are below the *true* quantitative infestations of the equines which were studied by us, since *all* of the worms were not recovered and identified. Mentally, the above figures might be uniformly corrected by some common factor—conservatively and amply estimated, perhaps, at about 20 per cent or 30 per cent. There is no reason to believe, however, that any of these considerations or limitations, detract from the scientific usefulness of these data.

Kind of Host and Size of Infestations.

The Strongylid infestations of the 17 horses covered by this survey varied from 36 to 1725 worms each, with an average of 834 per animal. For the 31 mules the range was from 74 to 4124 worms each, with an average of 856 worms per animal. It will be noted that these averages approximate closely the average for the entire series (849), it thus being indicated that both horses and mules are equally good hosts for at least most of the Strongylidae of equines.

Age of host and size of infestations.

It has been interesting to note that the infestations of the 33 animals which were 15 years of age or under ranged from 36 to 4124 worms each and averaged 1053 per animal. On the other hand, the infestations of the 15 animals which were 16 years of age or over varied from 48 to 1659 worms per animal with an average of 396 each. Further subdivisions in these age-groups may be summarized as follows:

Age-groups (yrs.)	No. Animals	Range in Infestation	Average
10 and under	11	163 – 3878	1105
11 to 15	22	36 – 4124	1028
16 to 20	9	168 – 1659	550
over 20	6	48 – 359	164
	48	36 – 4124	849

From these data, it appears that there was a definite trend toward lighter infestations in the older animals. Considering the fact that the animals from which these data are derived were reared under the same conditions throughout, it has seemed that there is indicated, to a rather marked degree, a definite age-resistance after about 15 years of age.

SUMMARY

1. Data have been presented upon the qualitative and quantitative occurrence of the Nematode parasites recovered at autopsy from 48 horses and mules imported into the Panama Canal Zone and owned by the P. C. Dept. of the U. S. Army.

2. In all, 39 Nematode species were recovered, 32 of which were of the family *Strongylidae*. These parasites are reported for the first time from Army equines of the Panama Canal Zone.

3. A discussion of the incidence, abundance, host-localization, and host-preference (horse or mule) of each species has been presented.

4. Most of the Strongylid fauna was accounted for by relatively few of the species. Of the species recovered, 15 were considered as "common" and 17 as "rare." The "common" species accounted for over 98 per cent of the Strongylid fauna.

5. Of the 32 different species of *Strongylidae,* in spite of the fact that all were demonstrated quantitatively to have preferred localizations in the large bowel, there were taken at one time or another 19 different species from the cecum, 26 from the ventral colon, and 27 from the dorsal colon.

6. The Strongylid infestations averaged 849 worms per animal. The number from the cecum averaged 127, from the ventral colon 486, from the dorsal colon 236.

7. There was an average of 15 different Strongylid species per animal. In the cecum the average was 5, in the ventral colon 11, in the dorsal colon 6.

8. There was an average of 2 to 3 species of extra-*Strongylidae* per host, which contributed, on the average, about 33 worms to the infestations.

9. It is believed that the infestations of these animals, as summarized in 6, 7, and 8 above, represent about the minimum practical level attain-

able by the intelligent application of the known methods of prevention and treatment.

10. A hypothetical infestation has been presented which summarizes both qualitatively and quantitatively many of the results of this survey. It also gives the typical Strongylid fauna of the cecum, ventral colon, and dorsal colon, respectively.

11. Horses and mules harbored about the same average infestations, although certain of the species showed a preference for one or the other of these hosts.

12. The older animals, particularly those over 15 years of age, harbored lighter infestations than the younger ones. This was interpreted as an indication of an age-resistance of equines against Strongylid parasites.

13. Larvae of *S. vulgaris,* the agent of verminous aneurysm and arteritis in equines were taken from branches of the Great Mesenteric Artery in 75 per cent of the cases.

14. One parasite, *Cylicostephanus poculatus,* apparently reported previously only from horses, is herein recorded from the mule.

15. A few brief discussions, apart from those already summarized, have been given upon problems of systematics, biological characteristics, economic importance, etc., of some of the parasites encountered.

16. The methods of autopsy and worm-collection which were employed during this study in making a quantitative approach to the study of the equine infestations have been described in detail.

References Cited

Boulenger, Charles L. 1916.—Sclerostome parasites of the horse in England. 1. The genera *Triodontophorus* and *Oesophagodontus.* Parasit., 8: 420–439.

1920.—Sclerostomes of the donkey in Zanzibar and East Africa. ibid., 12: 27–32.

1921.—Strongylid parasites of horses in the Punjab. ibid., 13: 315–326.

Cram, Eloise B. 1924.—A new Nematode, *Cylindropharynx ornata,* from the zebra, with keys to related Nematode parasites of the *Equidae.* Jour. Agri. Res., 28: 661–672.

Gough, L. H. 1908.—Notes on South African parasites. An. Rept. of the So. African Assoc. for the Adv. of Sci. (quoted from G. Theiler).

Ihle, J. E. W. 1920.—Een nieuwe *Cylicostomum*—soort (*C. brevicapsulatum*) uit den darm van het paard. Tijdschrift voor Diergeneeskunde, Deel 47, Aflevering 5, 182.

1922.—Over de verdeeling van het geslacht Cylicostomum. ibid., 49: 135–136.

1922a.—Report of the commission appointed to inquire into the sclerostomiasis in Holland. 1. Zoological part. Vol. 1. The adult Strongylids (Sclerostomes) inhabiting the large intestine of the horse. 118 pp. 131 figs. Nat. Printing office, The Hague.

Looss, A. 1901.—The *Sclerostomidae* of horses and donkeys in Egypt. (With 13 plates). Records of the Egyptian Gov't Faculty of Medicine, Cairo, Egypt. Vol. 1, pp. 21–114.

McIntosh, Allen. 1933.—Equine parasites from Puerto Rico. Jour. Parasit., 20: 110.

Skladnik, Jozef. 1935.—Sur la synonymie des quelques especes de la sous-famille des *Trichoneminae*. Ann. de Parasit., 13: 307–311.

1935a.—*Trichoneminae* u koni w polsce. odb. z. mies. "Wiadomosci Weterynaryjne" No. 177, 137–183. (with 25 plates and French summary).

Theiler, Gertrud. 1923.—The Strongylids and other Nematodes parasitic in the intestinal tract of South African Equines. 9th and 10th Repts. of the Director of Veterinary Education and Research, Dept. of Agri. Un. of So. Africa. April, pp. 603–773.

Wetzel, Rudolf. 1930.—On the biology of the fourth stage larva of *Oxyuris equi* (Schrank). Jour. Parasit., 17: 95–97.

Yorke, W. and J. W. S. Macfie. 1920.—*Strongylidae* in Horses. 11. Species found in West Africa and Jamaica. Ann. Trop. Med. Parasit., 14: 165.

RESEARCH NOTES

INOCULATION EXPERIMENTS WITH *TRICHOMONAS HOMINIS, T. BUCCALIS* AND *T. VAGINALIS*

These experiments were carried on in an effort to advance further proof that the human trichomonads (*Trichomonas hominis, T. buccalis* and *T. vaginalis*) are separate and distinct species. At the present time there is some uncertainty among medical men with regard to the distinctness of the three forms. It is important to determine definitely all criteria by which these three forms may be distinguished. Their specific distinctness has a direct bearing on the sources of the infections, as well as the mode of transmission. Since there are morphological similarities between the three forms, contributory evidence drawn from their biological activities adds to their diagnostic differences. With this in mind, we first attempted to infect experimentally the intestinal tract of six-weeks old kittens with a strain of *Trichomonas hominis*. This strain was then in culture in our laboratory in Locke's-Egg-Blood medium. Each animal had been previously examined and proven negative both by direct smear and by culture methods before being inoculated. Following an 18-hour period of fasting the kittens were inoculated by means of a rectal catheter, each animal receiving about 3.0 cc. of the culture.

One week following the inoculations the animals were autopsied and the caecum and ileum examined for Trichomonas. Cultures were also made at the same time in order to avoid the possibility of overlooking a light infection. Eleven kittens were inoculated in this manner, with positive results being obtained in eight animals, or 73% of the cases.

After thus proving that *T. hominis* from the human could be successfully established in the intestinal tract of kittens, attempts were made to determine if *T. vaginalis* and *T. buccalis* could likewise each be established in the *same* location. The eight cases of each species tried thus far have proven negative; *T. vaginalis* and *T. buccalis* both failing to survive in the intestinal tract of kittens. One inoculation each of *T. vaginalis* and *T. buccalis* directly into the ileum by means of laparotomy was also tried, but trichomonads were never recovered. A freshly isolated strain of *T. buccalis* was then put in the mouths of four kittens. Inoculations were made by gently scraping the gingival area around the gums and inserting a little of the culture. It was found that *T. buccalis* could be successfully established in the mouths of kittens, though showing but little evidence of pathogenicity there. *Trichomonas hominis* and *T. vaginalis* were each tried in the mouths of six kittens, but results in all cases proved negative. These three forms of Trichomonas were then successively tried in the mouths of four *Macacus rhesus* monkeys, but with negative results in all cases, for none of the three could be established there.

Attempts were then made to infect the vagina of eight cats with *T. vaginalis,* as well as with *T. hominis* and *T. buccalis,* but results were again negative with all three forms. Following this we attempted to infect with *T. vaginalis* the vaginal tract of six Norway rats, five guinea-pigs, three rabbits, and three wood rats, but were unsuccessful in all such attempts. The failure of *T. vaginalis* to take in the vagina of any one of these lower mammals may be due to the absence of glycogen in the vagina. In the human, glycogen is present in the wall, and according to some workers, it may be the glycogen which is acted upon by bacteria to produce the large amount of lactic acid which is present and hence causes the marked acidity of the human vagina, as opposed to the alkaline condition to be found in lower mammals.

The pH of the normal human vaginal tract by colorimetric methods is markedly acid, while electrometric pH determinations on the vagina of some laboratory animals by means of the glass electrode indicate a more or less high degree of alkalinity; in the Norway rat the pH runs about 7.0, in the guinea-pig, 7.2, and in the rabbit, 8.0.

Similar attempts to infect the vagina of four monkeys with *T. vaginalis* have failed, an inhibitory secretion apparently being present which is highly lethal to *T. vaginalis;* for in less than 24 hours after inoculation with a fresh virulent culture none of the flagellates were detected, either in fresh smear or by culture methods. Hegner (1928) has reported similar unsuccessful results in the monkey with *T. vaginalis* from the human. He has, however, successfully infected the vagina of monkeys with a species peculiar to the monkey which he calls *T. macacovaginae,* and which manifests in the monkey symptoms similar to those caused by *T. vaginalis* in the human.

The dissension concerning these three species is particularly important from a clinical standpoint. Various workers have reported incidence of *T. vaginalis* to be from 10% to 69%. Since the incidence of infection with *T. vaginalis* is fairly high, its pathogenicity unquestionable, and its mode of transmission unknown, the possibility of a vaginal infection arising from a previously existing buccal or intestinal infection should therefore either be proven or be definitely eliminated. Possibilities of reinfection are obviously greatly reduced if the three species are distinct and not transferable from organ to organ.

The failure of each of these three species of human Trichomonas to become established in any other location than that which constitutes the known normal habitat of each, as based upon animal inoculation experiments, gives additional proof of the distinctness of the three species. It also suggests a corresponding organ specificity in man, and that infection in man with *T. vaginalis* does not occur through previous infection with *T. buccalis* of the mouth or *T. hominis* of the intestine, but is from an outside source.

The author wishes to acknowledge the courtesy extended by Professor C. A. Kofoid, in whose laboratory this work was done.—Aileen E. Bonestell, *Department of Zoology, University of California.*

AN INFESTATION BY THE ORIENTAL RAT FLEA, *XENOPSYLLA CHEOPIS* ROTHSCHILD, IN MINNESOTA

There is a current opinion that the oriental rat flea, *Xenopsylla cheopis* Rothschild, is limited in its distribution in the United States to seaport cities. Roudabush and Becker (1934, Science, N. S., 80: 97) have shown that the species is established in the native wild rats in Iowa. Dr. William A. Riley, in a personal communication, states that several years ago he identified a flea taken from a rat at St. Paul, Minnesota, as belonging to this species. The observations here reported deal with a rather unique infestation of this flea at the University of Minnesota Farm, St. Paul.

Early in June, 1936, a worker at one of the dairy barns noticed an irritation on his ankles after being in the loft of this building. About July first the annoyance became so severe that an examination of the loft was made, revealing a heavy flea infestation. The fleas were so numerous that the worker picked approximately one hundred from his person after being in the loft but a few minutes. Two domestic cats living in the barn were found also to be heavily infested. On July 2, the worker treated the cats with a cresol solution, from which they died the following day. The attention of the writer was called to the abundance of fleas in this barn on July 7. An examination showed that the fleas in the loft were largely concentrated in a pile of empty burlap feed bags upon which the cats had habitually slept. Inquiry revealed that the barn had had a heavy rat population during the winter and that the cats were maintained as predators. A study of the fleas taken from the cats and those prevalent in the loft showed that they were all of the same species—*Xenopsylla cheopis* Rothschild.

The eradication procedure was very simple after the cats had been unintentionally destroyed. The feed bags were removed and fumigated with chloropicrin. The floor of the loft was then treated with cresol solution to destroy any of the

developmental stages that might be present. Following the control measures, a few fleas were noticed in the loft during the next week, but these disappeared. The barn and loft were again examined on July 27, but no fleas were found.

In view of the presence of this flea on native wild rats in Iowa and the earlier record from St. Paul, the most probable explanation for the origin of the present infestation is that the cats received the fleas from native rats.—WILLIAM B. OWEN, *Assistant Professor of Zoology, University of Wyoming.*

THE GENUS *SCHIZOTAENIA* IN PORCUPINES

Two species of the genus *Schizotaenia* have been recorded from North American porcupines. One, *S. americana,* was first described by Stiles (1895, Vet. Mag., 2: 341–346) from specimens collected from *Erethizon epixanthum* in Wyoming. It has subsequently been recorded by Beddard (1914, Proc. Zool. Soc., London, 1039–1055) from an *Erethizon dorsatum* which died in the London Zoo after 14 months' residence there; by Douthitt (1915, Ill. Biol. Mon., 1, No. 3) from an *E. dorsatum* from Michigan, and by Kilham (1931, Jour. Mam., 12: 318–319) from an *E. dorsatum* from New Hampshire.

The other species is *Schizotaenia variabilis,* differentiated by Douthitt (1915), who recognized that some material collected by A. K. Fisher from *E. dorsatum* at Lake George, N. Y., and referred by Stiles (1896, Proc. U. S. Nat. Mus., 19: 145–235) to *S. americana,* could not be included in that species. Douthitt correctly concluded that some specimens described by Cohn (1906, Centbl. f. Bakt., 1, Orig., 40: 362–367) from *Erethizon epixanthum* in Alaska and referred by him to *S. americana* were really *S. variabilis.*

The specimens described by Beddard (1914) were placed by him in a new genus and species, *Monoecocestus erethizontis.* Two of Beddard's specimens were reëxamined by Baer (1925, Ann. Trop. Med. and Parasit., 19, 1–22) who came to the conclusion that Beddard's worms not only belonged to the genus *Schizotaenia,* but represented a mixture of the two species *americana* and *variabilis.* Since Beddard's name *erethizontis* preceded Douthitt's name *variabilis,* Baer accepted *erethizontis* as valid for this species, *variabilis* becoming a synonym. The justification for considering Beddard's material a mixture of two species is not mentioned. In his paper Beddard states that he obtained a large number of specimens of the worm he described; these reached a length of 50 to 60 mm. or a little more, and their "greatest breadth is not more than just over 3 mm." He also states that the ovary "is near the middle of the proglottid, verging towards the pore side." These two characters are sufficient to prove that the specimens Beddard described, whether or not there were others mixed with them, were *Schizotaenia americana,* of which *Monoecocestus erethizontus* therefore becomes a synonym.

The writer obtained many hundreds of specimens of each of these two species of Schizotaenia from a specimen of *Erethizon epixanthum* near Crested Butte, Colorado, at an elevation of 9500 feet. At the time of collection it was not realized that two species were present, so no information is available as to relative distribution in the intestine. The two species are readily distinguishable by the naked eye, adult specimens of *S. americana* being 30 to 60 mm. long with a maximum width of 3 to 4.5 mm. (Stiles gives 6 mm.), while adult *S. variabilis* are 33 to 42 mm. long (Douthitt gives 20 mm.) and 7.5 to 9.5 mm. in maximum width. The ovaries of *S. americana* are always broadly overlapping, while those of *S. variabilis* are so widely displaced from the center of the proglottids that their inner extremities rarely reach the median line. It is evident that these two species each have a wide distribution in North America and are found indiscriminately in both of the North American species of porcupine.—ASA C. CHANDLER, *Biological Laboratory, Rice Institute, Houston, Texas.*

OVIPOSITION BY *CULICOIDES* BREEDING IN SALT MARSHES

By means of a method recently devised, species of sand flies breeding in salt marshes along the southeastern coast of the United States have been induced to deposit eggs under laboratory conditions. The species *Culicoides canithorax* Hoff., *C. dovei* Hall, and *C. melleus* Coq. were collected in the field at night. Numerous specimens were attracted to the lights of an automobile, in front of which they were captured by sweeping with a net. These specimens were transferred to jars, brought into the laboratory, and the sand flies passed through a screen into glass lamp chimneys. The positive phototropism of *Culicoides* proved of advantage when these transfers were being made. To prevent larger insects captured with the sand flies from entering the chimneys, 18-mesh screen was placed between the jar and the chimney. One end of each chimney was covered with cheesecloth and the other placed on moist blotting paper, or on moist marsh soil in a Petri dish.

A meal of human blood was given the sand flies within 12 hours of the time they were collected. No different observations were recorded when more than one feeding was allowed, either in the length of life or in the number of eggs produced. At times one or two eggs have been found 2 days or less after collection and this seems an indication that feeding had taken place prior to capture. Oviposition among a group was found to take place from 4 to 10 or 12 days subsequent to the first blood meal. Masses of as many as 30 eggs, as well as single eggs, were noted on the surface of moist soil and on moist blotting paper. The sand flies were observed to die before, during, and after ovipositing. Dissection revealed varying numbers of eggs within the abdomens of the dead females.

Hatching of eggs has taken place as early as 4 or 5 days after oviposition. Some eggs, however, did not hatch until after longer periods. Eggs hatched when kept on blotting paper moistened with distilled water and when placed in distilled water. Larvae from these died in less than 24 hours, but larvae that hatched in salt-marsh water lived for several days.

Previously, oviposition by species of this genus that breed in salt marshes had never been witnessed, and the only eggs seen were a very few obtained artificially. —F. O. Atchley and J. B. Hull, *U. S. Department of Agriculture, Bureau of Entomology and Plant Quarantine.*

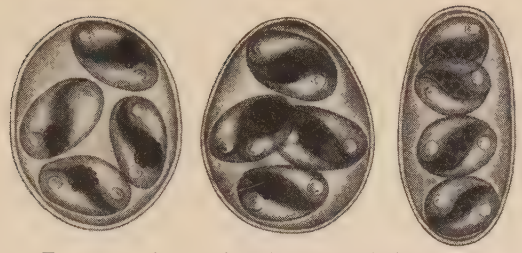
COCCIDIOSIS IN THE KANGAROO

Wenyon and Scott (1935, Trans. R. Soc. Trop. Med. Hyg., 19: 7–8) were the first investigators to refer to coccidia in the kangaroo (*Macropus bennetti*). They named their species *Eimeria macropodis.* The next year Triffit (1926, Parasitol., 18: 31–46) studied this material and described the development of the organism during schizogony and sporogony, including the oocysts, which were oblong and asymmetrical (one side being more convex than the other). One end showed a very distinct micropyle 3μ broad. The membrane consisted of three layers of which the middle was the broadest (about 1μ in thickness) and was transversely striated. The oocyst measured 22 to 34μ by 10 to 17μ. After 48 hours sporocysts (7 by 11μ by 6 to 8μ), with one end pointed, were developed. Residual bodies were present in the sporocysts, although not in the oocysts.

In February and March, 1935, the present writers examined the feces of two kangaroos (*Macropus giganteus*), sent by the veterinarian K. S. Kolomietz from the Khartov Zoo. The feces were prepared with a solution of potassium bichromate, following the method of Darling. Oocysts in considerable numbers were found in both animals, and two distinct species were discovered.

Description of the first species, Eimeria marsupialium n. sp. (Figs. 1 and 2).

The oocyst was oblong, seldom oval. There was a double membrane, each portion having a thickness of 1μ. Some specimens had a slight thinning of the membrane at one end, but no micropyle was found. The color was yellowish. Measurement of 77 oocysts provided the following measurements: greatest size,



FIGS. 1 and 2. *Eimeria marsupialium* n. sp.
FIG. 3. *Eimeria fausti* n. sp.

26 by 20μ; smallest size, 20 by 16μ; average size, 22.2 by 18.0μ. Ratio of length to breadth: 1 : 0.67–0.97; average, 1 : 0.8; commonly found, 1 : 0.81. In the ripe cysts there were 4 round sporoblasts, which later changed into spores measuring 8 to 12μ by 6 to 8μ, having a contoured membrane and lacking Schneider bodies. The oocysts had neither residual nor polar bodies; residual bodies were found only in the sporocysts.

This organism was definitely different in shape and structure from *Eimeria macropodis* and for it the writers propose the name *Eimeria marsupialium* n. sp.

Description of the second species, Eimeria fausti n. sp. (Fig. 3).

In one of the kangaroos a few specimens of a different type were discovered. The oocysts were cylindroidal in shape, with rounded ends, and were hyaline. Their membrane was smooth, with a thickness of 0.5μ. They measured 22 to 24μ by 12 to 14μ, with a ratio of 1': 0.50–0.58. Within each ripe oocyst there developed 4 spores, measuring 6 to 8μ by 6μ. Each sporocyst produced 2 sporozoites. Residual bodies were found only in the sporocysts. Sporulation of the oocysts required considerably less time than it did for *E. marsupialium.*

Although superficially resembling *Eimeria macropodis* this species differs in size and in length-breadth ratio, and for it the writers propose the name, *Eimeria fausti* n. sp., in honor of the American parasitologist, Professor Ernest Carroll Faust.—PROFESSOR W. L. YAKIMOFF AND S. N. MATSCHOULSKY, *Parasitology Laboratory, Veterinary School, Leningrad, U. S. S. R.*

THE AMPHIPOD, *ORCHESTIA PLATENSIS,* AN INTERMEDIATE HOST FOR *HYMENOLEPIS EXIGUA,* A TAPEWORM OF CHICKENS IN HAWAII

During a recent examination of several invertebrates collected from various poultry farms near Honolulu, the writer discovered that an amphipod, *Orchestia platensis,* was frequently parasitized by many cysticercoids (Fig. 1, a). Four one-day-old chicks fed with several infested amphipods and killed 21 days after experimental feeding showed many adult tapeworms embedded in the wall of the anterior portion of the small intestine; four control chicks kept under the same condition as the other four chicks involved in the feeding experiment remained free of all helminths. The adult tapeworms recovered from the experimental infected chicks were identified as *Hymenolepis exigua.*

The adult tapeworms have been previously reported from chickens only in Asia (Japan and Formosa), and the life history of these parasites was heretofore unknown. Two of the cysticercoids recovered from the naturally infested amphipods measured 290 to 330μ in length and 267 to 282μ in width. The rostellum is provided with 10 hooks (Fig. 1, b), each hook being 45μ long; each of the four suckers measures about 56μ in diameter. The larva is surrounded by a cyst wall possessing a more or less slender appendage or tail; the six embryonal hooklets are usually visible near the tip of this appendage.

Since the completely developed egg of this parasite has not previously been described, a brief description follows: Embryophore (Fig. 1, c) rounded, about

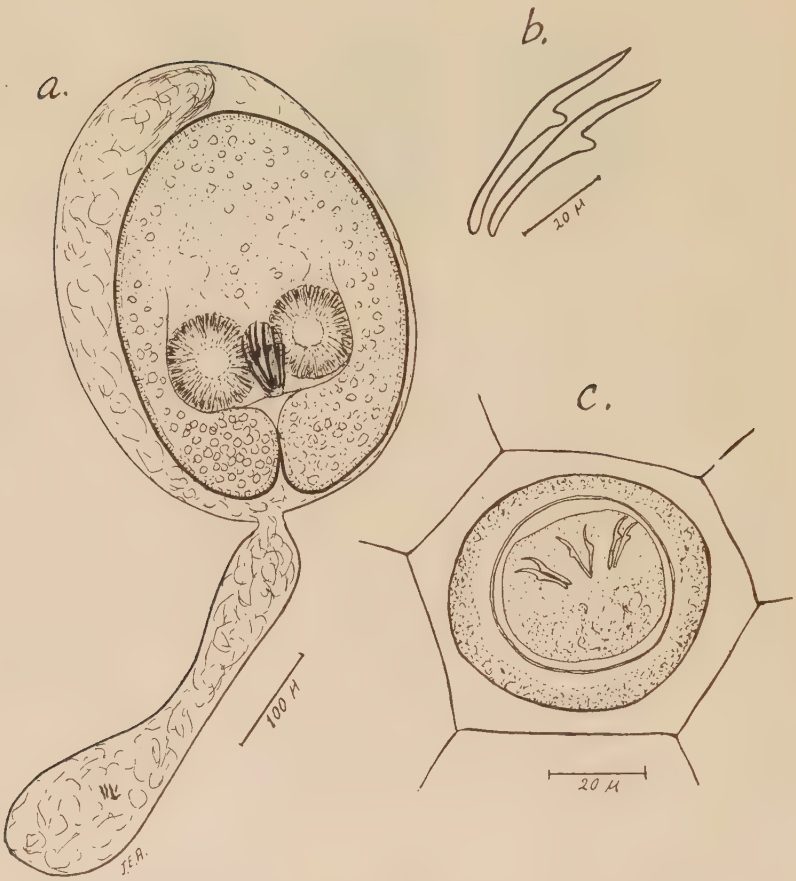


FIG. 1. *Hymenolepis exigua.*—(a) Mature cysticercoid from *Orchestia platensis;* (b) Two of the hooks from the rostellum of the cysticercoid; (c) Egg from the adult tapeworm surrounded by an uterine capsule.

50 to 57μ in diameter; Onchosphere about 30 to 32μ in diameter, and possessing 6 hooklets, each about 13μ long.

Hymenolepis exigua has been noted frequently by the writer in chickens in the island of Oahu. The amphipod which serves as intermediate host is of common occurrence in some poultry farms, especially in damp and wet areas around water fountains. Out of 50 amphipods collected on a poultry farm near Honolulu, 32, or 64 per cent, were found naturally infested with the cysticercoids of *H. exigua.*

The writer is indebted to Dr. E. E. Wehr, of the Zoological Division of the Bureau of Animal Industry, U. S. Department of Agriculture, for the identification of the adult tapeworm, and to Dr. M. A. Miller, of the University of Hawaii, for the identification of the amphipod.—JOSEPH E. ALICATA, *Hawaii Agricultural Experiment Station, University of Hawaii.*

A NEW SPECIES OF TREMATODE, *CERCORCHIS CRYPTOBRANCHI,* FROM *CRYPTOBRANCHUS ALLEGANIENSIS*

In the examination of specimens of *Cryptobranchus alleganiensis,* from Ames, Iowa, flukes belonging to the genus *Cercorchis* Lühe, 1900, were found in the in-

testines. Members of this genus are common parasites of reptiles. Only two species have been reported from Amphibia, *i.e., Cercorchis stunkardi* Chandler, 1923 (Proc. U. S. Nat. Mus., 63: 1–7) and *Cercorchis necturi* Perkins, 1928 (Parasit., 20: 336–356). With the exception of *Cercorchis solivagus* Odhner, one of the outstanding differences between the members of the genus found in Amphibia and those found in reptiles is that the acetabulum is larger than the oral sucker in the former. The trematodes from *Cryptobranchus* show this same peculiarity, but upon comparing them with the two above mentioned species it was found that marked differences made it necessary to establish a new species, *Cercorchis cryptobranchi.*

Cercorchis cryptobranchi n. sp. (Fig. 1)

Specific diagnosis:—Characters of the genus: Adult averages 5.13 × 0.64 mm., with fine spines at anterior end extending back to about half way between the oral sucker and the acetabulum. Oral sucker smaller, 0.135 × 0.158 mm., than the acetabulum, 0.154 mm. in diameter. Prepharynx very short and esophagus longer than pharynx. Pharynx about 0.097 mm. in diameter. Intestinal ceca extend beyond the testes to posterior end. Cirrus well developed, extending back to region

FIG. 1. Adult of *Cercorchis cryptobranchi* n. sp.

of the ovary but is usually separated from it by loops of the ascending uterus. Genital pore anterior to acetabulum and slightly to the left of the median line. Testes about the same size, 0.285 mm. in diameter. Ovary, 0.163 mm. in diameter, near median line and just anterior to oötype. Vitellaria follicular, extending from the acetabular region to the anterior portion of the posterior quarter of the body. They are indistinctly divided into groups, 8–10 on the right side and 11–12 on the left. Coils of uterus fill region between ovary and anterior testis. Ascending and descending loops adjacent and may overlap the intestinal ceca. Metraterm well developed, extending back to about the end of the prostatic region of the cirrus. The eggs measure 0.038 × 0.019 mm.

Host.—Cryptobranchus alleganiensis.

Location.—Intestine.

Locality.—Ames, Iowa.

The above measurements were obtained by averaging the dimensions of eighteen adult specimens. *Cercorchis cryptobranchi* differs from both of the other members of the genus, which have been found in Amphibia, in having the vitellaria extending much farther forward. *Cercorchis necturi* Perkins, 1928, is about twice as broad, its suckers are larger and the eggs smaller. In *Cercorchis stunkardi* the suckers are much larger, especially the acetabulum, and the eggs are larger. —DONALD B. MCMULLEN, *Biology Department, Monmouth College,* and ROBERT L. ROUDABUSH, *Department of Zoology and Entomology, Iowa State College.*

ARTHROPOD AND HELMINTH PARASITES OF THE AMERICAN BISON (*BISON BISON*)

The cooperation of the Biological Survey made possible a study of the parasites of the bison on the Wichita National Game Preserve, Cache, Oklahoma. Thirteen apparently normal animals were slaughtered, December 12 and 13, 1935, for sale, and each of these was examined, both internally and externally, for parasites. Hurried examinations were made in the field without laboratory facilities. Hence, the number of parasites found is probably not indicative of

the total infestation. The animals were part of a herd of 300. The herd had 3,000 acres of pasture on which to range. Cattle were not allowed to range on the same ground, and any intermingling of cattle and the buffaloes was temporary and accidental.

Below is a table showing the accession number, age and sex of each bison killed, with the parasites found in or on it.

TABLE I.—*Arthropod and Helminth Parasites from American Bison*

Buffalo Number	Age (in Yrs.) and Sex	*Dermacentor nigrolineatus**	*Hypoderma lineatum* Instars			*Moniezia benedeni*	*Haemonchus contortus*		*Dictyocaulus hadweni**		*Oesophagostomum radiatum**
			1.	2.	3.		♀	♂	♀	♂	
1.	3 ♂			5	15						
2.	2 ♂	1 ♀	1	5	25						
3.	2 ♂	1 ♀		2	10	13					
4.	2 ♂				3	52	17	11			
5.	2 ♂			2	10						
6.	2 ♂			5	5		28	9			
7.	2 ♂			3	10		6	0			
8.	4 ♂					2	13	1			1
9.	3 ♂			1	9		2	0			
10.	3 ♂			5	4						
11.	3 ♂			2	3		24	7			
12.	2 ♂		1	8	16	10	24	19			
13.	5 ♀		present but not collected			10	1	0	1	1	

* Determined through the courtesy of Dr. Benjamin Schwartz Bureau of Animal Industry, Washington, D. C.

In addition to what is shown in the table, blood examinations were made from each specimen but no parasites were found.

The author wishes to express his appreciation for the cooperation of Dr. I. N. Gabrielson, Head of the Biological Survey; Mr. H. H. French, Director of the Wichita National Game Preserve; Mr. Earl Drummond, Ranger, and all the members of the staff at the Wichita Preserve. Mr. G. A. Smith, who purchased the buffaloes, was extremely kind in regulating the routine and permitting examination of the animals. Thanks are also tendered to Dr. A. M. Lucas, of Iowa State College, who assisted in no small measure in collecting the material. Journal Paper No. 375 of the Iowa Agricultural Experiment Station, Ames, Iowa. Project No. 46. In cooperation with the Iowa State College, U. S. Biological Survey and the Wildlife Institute.—ROBERT L. ROUDABUSH, *Department of Zoology and Entomology, Iowa State College.*

OCCURRENCE OF HAEMATOZOA IN SOME CALIFORNIA COLD-BLOODED VERTEBRATES

During the past five years the writers have examined the blood of 34 species and subspecies of poikilothermic vertebrates involving 349 individuals from central and southern California. The studies were started at the University of California at Berkeley and have been continued recently at Los Angeles Junior College and the University of California at Los Angeles. Most of the specimens were collected by the authors but thanks are due Messrs. A. E. Peterson, W. Marshall, Harlan Wood, H. Michener, and L. M. Klauber for certain forms.

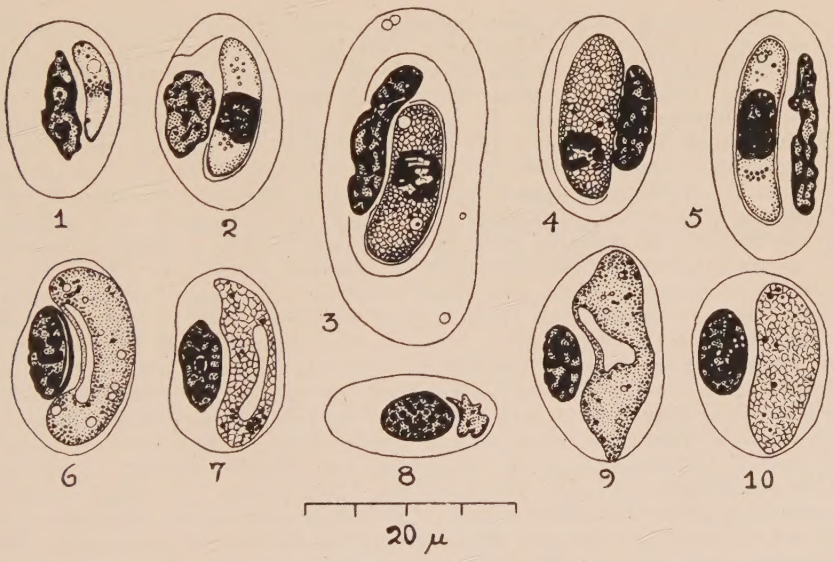
The true identity of many of the parasites is unknown since the material at hand gives only meager information as to the complete life cycle. The authors hope to clear up some of this difficulty by further studies on the forms already discovered.

The fishes examined were all negative. They include 2 Sacramento Perch, *Archoplites interruptus*; 2 Square-tail Catfish, *Ameiurus nebulosus*; 2 Sacramento Suckers, *Catostomus occidentalis,* all from the San Joaquin River, near Stockton, San Joaquin County.

The amphibians examined were also negative. They include the following: 1 Yosemite Park Toad, *Bufo canorus,* Yosemite, Mariposa County; 2 Slender Salamanders, *Batrachoseps a. attenuatus,* Berkeley, Alameda County; 4 California Yellow-legged Frogs, *Rana b. boylii,* Mt. Diablo, Contra Costa County; 7 California Red-legged Frogs, *Rana aurora draytonii,* (4) Mt. Diablo, Contra Costa County and (3) Pasadena, Los Angeles County; 7 Garden Salamanders, *Batrachoseps pacificus major,* Pasadena, Los Angeles County; 3 Pacific Tree-toads, *Hyla regilla,* Pasadena, Los Angeles County; and 4 California Toads, *Bufo boreas halophilus,* (2) Pasadena and (2) Los Angeles, Los Angeles County.

A malaria-like organism, *Plasmodium* (figs. 6, 7), has been found in 19 of 228 Pacific Blue-bellied Lizards, *Sceloporus o. occidentalis.* Eighteen of 178 from Berkeley, Alameda County, and 1 of 34 from Mt. Diablo, Contra Costa County were infected. One of 4 Mountain Swifts, *S. graciosus gracilis,* from Gualala River, Sonoma County was infected with *Plasmodium* (figs. 8–10).

Several reptiles were infected with haemogregarine-like organisms, *Karyolysus* (?) (figs. 1–5). These include 2 of 4 Northern Crested Lizards, *Dipsosaurus d. dorsalis,* and 1 Red Racer, *Masticophis flagellum frenatus,* from Palm Springs, Riverside County; 1 Pacific Rattlesnake, *Crotalus confluentus oregonus,* from Glendale, Los Angeles County and 1 Coast Garter Snake, *Thamnophis ordinoides atratus,* from La Fayette, Contra Costa County.



EXPLANATION OF FIGURES

All figures were drawn with the aid of a camera lucida. Magnification, ×1235. Jenner-Giemsa strain.

FIG. 1. Gametocyte of *Karyolysus* (?) in erythrocyte of Northern Crested Lizard, *Dipsosaurus d. dorsalis.* Cytoplasm of parasite is homogeneous and strains pale blue. Vacuole is pinkish and adjacent granular clump of chromatin strains purple. A few dark violet granules occur in cytoplasm. Cytoplasm of erythrocyte shows lighter-straining areas.

FIG. 2. Gametocyte of *Karyolysus* (?) in erythrocyte of Pacific Rattlesnake, *Crotalus confluentus oregonus*. Cytoplasm pale blue with few fine violet granules. Clump of eosinophil granules below nucleus and at upper end of parasite. Compact nucleus. Cyst membrane present. Cytoplasm of erythrocyte shows pale areas.

FIG. 3. Gametocyte of *Karyolysus* (?) in erythrocyte of Pacific Rattlesnake, *Crotalus confluentus oregonus*. Advanced stage. Cytoplasm of parasite more dense and granular than fig. 2. Cyst membrane present. Zone of darker-straining cytoplasm surrounds parasite and nucleus of blood cell. Blood cell is much hypertrophied, its cytoplasm is vacuolated and strains pale blue, indicating absence of hemoglobin.

FIG. 4. Gametocyte of *Karyolysus* (?) in erythrocyte of Red Racer, *Masticophis flagellum frenatus*. Parasite and host cell show same straining qualities as fig. 3.

FIG. 5. Gametocyte of *Karyolysus* (?) in erythrocyte of Coast Garter Snake, *Thamnophis ordinoides atratus*. Slightly granular cytoplasm stains pale blue, shows few pale violet granules. Compact nucleus. Cyst membrane present.

FIGS. 6–10. *Plasmodium* in erythrocytes. Figs. 6 and 7 from Pacific Blue-bellied Lizard, *Sceloporus o. occidentalis*, figs. 8–10 from Mountain Swift, *S. graciosus gracilis*. Figs. 6, 8, 9 show fairly homogeneous, deep blue cytoplasm. Figs. 7 and 10 show granular cytoplasm and stain pale blue with pale pinkish areas. Figs. 6 and 7 contain brownish black pigment granules. Figs. 8–10 show violet granules, but no pigment granules.

The following reptiles were negative: 209 Pacific Blue-bellied Lizards, *Sceloporus o. occidentalis*, (160) from Berkeley, Alameda County, (33) Mt. Diablo and (5) Moraga, Contra Costa Conty, (3) near Soda Springs, Placer County, (3) Ben Lomond, Santa Cruz County, (5) Fairfax, Marin County; 17 Western Blue-bellied Lizards, *S. occidentalis biseriatus*, (3) from Sequoia National Park, Tulare County, (7) near Mt. Wilson, Los Angeles County, (3) Pasadena, Los Angeles County, (4) Lebec, Kern County; 6 Tenaya Blue-bellied Lizards, *S. occidentalis taylori*, (4) from North Fork of Stanislaus River, Calaveras County and (2) Yosemite National Park, Mariposa County; 4 Sagebrush Swifts, *S. g. graciosus*, Soda Springs, Placer County; 3 Mountain Swifts, *S. graciosus gracilis*, from Gaulala River, Sonoma County; 14 Desert Scaly Lizards, *S. magister*, Neenac, Los Angeles County; 2 Northern Crested Lizards, *Dipsosaurus d. dorsalis*, from Palm Springs, Riverside County; 2 San Francisco Alligator Lizards, *Gerrhonotus c. coeruleus*, Ben Lomond, Santa Cruz County; 3 Sierra Alligator Lizards, *Gerrhonotus coeruleus palmeri*, Sequoia National Park, Tulare County; 1 Desert Horned Toad, *Phrynosoma platyrhinos*, 3 Chuckwallas, *Sauromalus obesus*, and 1 Desert Whip-tail Lizard, *Cnemidophorus t. tesselatus*, all from Coachella Valley, Riverside County; 1 Stejneger's Whip-tail Lizard, *C. tesselatus stejnegeri*, Pasadena, Los Angeles County; 2 Banded Geckos, *Coleonyx variegatus*, Dry Lake near Kane Springs, San Diego County; 2 Southern Brown-shouldered Lizards, *Uta stansburiana elegans*, Pasadena, Los Angeles County; 6 California Brown-shouldered Lizards, *U. s. hesperis*, (2) Pasadena and (1) near Mt. Wilson, Los Angeles County, (3) Lebec, Kern County; 1 Gridiron-tailed Lizard, *Callisaurus v. ventralis*, Coachella Valley, Riverside County; 2 Desert Night Lizards, *Xantusia vigilis*, Palmdale, Los Angeles County; 6 Mearns' Giant Uta, *Uta mearnsi*, Palm Springs, Riverside County; 1 San Diegan Gopher Snake, *Pituophis catenifer annectens*, March Field, Riverside County; 1 Spotted Night Snake, *Hypsiglena ochrorhynchus*, Berkeley, Alameda County; 1 Pacific Rattlesnake, *Crotalus confluentus oregonus*, Berkeley, Alameda County and 2 Coast Garter Snakes, *Thamnophis ordinoides atratus*, (1) Berkeley and (1) Thornhill Pond, Alameda County.—SHERWIN F. WOOD AND FAE D. WOOD, *Department of Zoology, University of California, Los Angeles, Calif.*

ERRATA IN PAPER BY H. W. STUNKARD.

"THE MORPHOLOGY AND LIFE HISTORY OF *PLAGITURA PARVA* STUNKARD, 1933 (TREMATODA)."

J. P., Vol. 22 (4), pp. 354–374.

P. 354, par. 3, line 3, "left" should read "eft."
P. 356, par. 4, line 2, "metacercaria" should read "metacercariae"; "cercaria" should read "cercariae."
P. 363, par. 2, line 5, "newts" should read "snails"; line 6, "snail" should read "newt."
P. 365, par. 1, line 17, "natural" should read "neutral."
P. 366, par. 3, line 3, "Mandistomum" should read "Manodistomum"; par. 4, line 12, "genue" should read "genus."

Portraits of
Parasitologists

Published originally in the
JOURNAL OF PARASITOLOGY
Printed on Plate Paper Ready for Framing

Nathan Augustus Cobb, from September 1932 issue
Col. Charles F. Craig, from February 1936 issue
Samuel Taylor Darling, from March 1926 issue
Friedrich Fülleborn, from June 1934 issue
Maurice Crowther Hall, from March 1933 issue
Isao Ijima, from March 1924 issue
Joseph Leidy, from September 1923 issue
Nils Johan Teodor Odhner, from December 1929 issue
Stanislaus von Prowazek, from December 1915 issue
Brayton Howard Ransom, from September 1926 issue
Francis Metcalf Root, from April 1935 issue
Theobald Smith, from August 1935 issue
Charles Wardell Stiles, from June 1933 issue
William Hay Taliaferro, from March 1934 issue
Ernest Edward Tyzzer, from February 1935 issue
Henry Baldwin Ward, from December 1932 issue

25 cents each

Sent post paid on receipt of cash with order

Address

Journal of Parasitology

615 N. Wolfe Street,
Baltimore, Md.

Lime & Green Sts.,
Lancaster, Pa.